# RECORDS OF THE AUSTRALIAN MUSEUM



# RECORDS OF THE AUSTRALIAN MUSEUM

Director: Mike Archer

Editor: Shane F. McEvey

# **Editorial Committee:**

 $S.T.\ Ahyong\ (Invertebrate\ Zoology)$ 

V.J. Attenbrow (Anthropology)

D.J. Bickel (Invertebrate Zoology)

G.D. Edgecombe (PALAEONTOLOGY)

S. Ingleby (Vertebrate Zoology)

J.M. Leis (Vertebrate Zoology)

S.F. McEvey (Invertebrate Zoology)

M.S. Moulds (Invertebrate Zoology)

F.L. Sutherland (Geology)

Chair: G.D.F. Wilson (Invertebrate Zoology)

© 2003 Australian Museum

The Australian Museum, Sydney

No part of this publication may be reproduced without permission of the Editor.

Published 10 December 2003

Price: AU\$50.00

Printed by RodenPrint Pty Ltd, Sydney

ISSN 0067-1975

The Australian Museum's mission is to research, interpret, communicate and apply understanding of the environments and cultures of the Australian region to increase their long-term sustainability. The Museum has maintained the highest standards of scholarship in these fields for more than 175 years, and is one of Australia's foremost publishers of original research in anthropology, geology and zoology.

The Records of the Australian Museum (ISSN 0067-1975) publishes the results of research on Australian Museum collections and of studies that relate in other ways to the Museum's mission. There is an emphasis on Australasian, southwest Pacific and Indian Ocean research. The Records is released annually as three issues of one volume, volume 54 was published in 2002. Monographs are published about once a year as Records of the Australian Museum, Supplements. Supplement 28 (ISBN 0 7347 2313 X) was published in June 2003. Catalogues, lists and databases have been published since 1988 as numbered Technical Reports of the Australian Museum (ISSN 1031-8062). Technical Report number 17 was published in March 2003. Australian Museum Memoirs (ISSN 0067-1967) ceased in 1983.

These three publications—Records, Supplements and Technical Reports—are distributed to libraries throughout the world and are now uploaded at our website six months after they are published. Librarians are invited to propose exchange agreements with the Australian Museum Research Library. Back issues are available for purchase direct from the Australian Museum Shop.

Authors are invited to submit manuscripts presenting results of their original research. Manuscripts meeting subject and stylistic requirements outlined in the *Instructions to Authors* are assessed by external referees.

www.amonline.net.au/publications/

Back issues may be purchased at the Australian Museum Shop or online at

www.amonline.net.au/shop/

The **cover illustrations**—by Francisco Neira—are of the holotypes of *Plectranthias robertsi* (above), *P. pallidus* and *P. lasti* (below) all collected from Australian waters by Australian Museum scientists. *Plectranthias pallidus* is known only from this specimen: bottom trawled from RV *Soela* off Townsville by McGrouther and Reader. These fish species are described by Randall & Hoese in *Records of the Australian Museum* 47(3). The faded impression (original photo by G.C. Clutton) of a Solomon Islands skink lizard—*Tribolonotus ponceleti* Kinghorn, 1937—which was also first described in an earlier issue of *Records of the Australian Museum* 20(1) provides background.

Australian Museum Scientific Publications is committed to open access to the scientific literature and, since 1999, our three serial titles have been released as PDF files, free of charge, at our website. These and many other works may also be purchased as bound issues from the Australian Museum Shop.

# An Appraisal of the Cicadas of the Genus *Abricta* Stål and Allied Genera (Hemiptera: Auchenorrhyncha: Cicadidae)

M.S. MOULDS

Invertebrate Zoology Division, Australian Museum, 6 College Street, Sydney NSW 2010, Australia maxm@austmus.gov.au

ABSTRACT. The cicada genus *Abricta* Stål currently contains a heterogeneous group of species which is considered best divided into four genera. *Abricta* sensu str. includes only *A. brunnea* (Fabricius) and *A. ferruginosa* (Stål) which are confined to Mauritius and neighbouring islands. The monotypic genus *Chrysolasia* n.gen., is proposed for a single Guatemalan species, *A. guatemalena* (Distant). Another monotypic genus, *Aleeta* n.gen., is proposed for the species *A. curvicosta* (Germar) from eastern Australia. Fourteen Australian species are placed in *Tryella* n.gen.: *castanea* Distant, *noctua* Distant, *rubra* Goding & Froggatt, *stalkeri* Distant, *willsi* Distant, *adela* n.sp., *burnsi* n.sp., *crassa* n.sp., *graminea* n.sp., *infuscata* n.sp., *kauma* n.sp., *lachlani* n.sp., *occidens* n.sp. and *ochra* n.sp.

The five remaining species currently placed in *Abricta* (borealis Goding & Froggatt, burgessi Distant, cincta Fabricius and occidentalis Goding & Froggatt from Australia plus pusilla Fabricius of unknown locality) do not belong to *Abricta* or closely allied genera.

Cladistic analyses place *C. guatemalena* basally on all trees. The Mauritian genus *Abricta* sensu str., and the genera, *Abroma* Stål and *Monomatapa* Distant, form a sister group to all Australian species. There is strong evidence suggesting that *Abricta* and *Abroma* are synonymous.

Keys to genera and species and maps of distribution are provided.

MOULDS, M.S., 2003. An appraisal of the cicadas of the genus *Abricta* Stål and allied genera (Hemiptera: Auchenorrhyncha: Cicadidae). *Records of the Australian Museum* 55(3): 245–304.

The genus *Abricta* belongs to the tribe Taphurini and previously included 14 described species distributed through Australia, Mauritius, and Guatemala. The largest of these, *A. ferruginosa* (Stål) from Mauritius, attains a wingspan of over 100 mm while the smallest, now *Tryella castanea* (Distant) from Australia, has a wingspan of around 45 mm.

The historical review below shows that species of *Abricta* have been described on an ad hoc basis with no real assessment of generic limits. Many of the species descriptions lack detail and some important morphological characters have never been examined. Perusal of museum

specimens suggested that *Abricta* was not be a coherent generic group and highlighted many difficulties in identifying Australian specimens.

Abricta Stål is here redefined to include just two species that are found only in Mauritius. The genus *Chrysolasia* n.gen. is established to accommodate the single Guatemalan species. Two genera are erected for the Australian species: *Aleeta* n.gen. which includes *curvicosta* Germar only, while the remainder are placed in *Tryella* n.gen. Nine new species of *Tryella* are described from Australia, making a total of 14. It has been necessary to place considerable emphasis

on male genitalic structures in distinguishing these taxa as other morphological features provide insufficient characters.

The name "Abricta complex of genera" is introduced for the complex of the following related genera: Abricta, Aleeta, Tryella, Chrysolasia, Abroma Stål and Monomatapa Distant. The primary purpose of this revision is to review the Australian species of this complex. An appraisal of the generic status of the many species falling within Abroma has not been attempted; nor has an assessment of the possible synonymy of Abroma with Abricta as suggested by Boulard (1979, 1990). Species no longer considered as belonging to Abricta are listed and will be transferred to other genera in a forthcoming work (Moulds, in prep).

Abbreviations used for names of collectors are as follows: AMW-H, A. & M. Walford-Huggins; GAD, G. & A. Daniels; MBM, Max & Barbara Moulds. Abbreviations for depositories of specimens are as follows: AE, collection of A. Ewart, Brisbane; AM, Australian Museum, Sydney; ANIC, Australian National Insect Collection, Canberra; ASCU, Agricultural Scientific Collection Unit, NSW Agriculture, Orange; BMNH, The Natural History Museum, London (also known as British Museum of Natural History); DPIB, Department of Primary Industries, Boroka; JM, collection of J. Moss, Brisbane; JO, collection of J. Olive, Cairns; K, Australian Museum registration numbers are prefixed "K"; LG, collection of L. Greenup, Sydney; LP, collection of L. Popple, Brisbane; MC, collection of M. Coombs, Brisbane; MM, Macleay Museum, University of Sydney: MNHP, Museum National d'Histoire Naturelle, Paris; MSM, author's collection; MV, Museum of Victoria, Melbourne; NMC Nationalmuseet, Copenhagen; NTM, Northern Territory Museum of Arts and Science, Darwin; OUM, Oxford University Museum, Oxford; PH, collection of P. Hutchinson, Perth; QM, Queensland Museum, Brisbane; RE, collection of R. Eastwood, Brisbane; SAM, South Australian Museum, Adelaide; UQIC, University of Queensland Insect Collection, St Lucia, Brisbane; UZMC, Universitets Zoologiske Museum, Copenhagen; WAM, Western Australian Museum, Perth; ZMH, Zoologischen Museums, Hamburg. Standard abbreviations are used for frequently used words, for example, creek (Ck), crossing (x-ing), homestead (Hsd), mile or miles (mi), near (nr), river (R.) and the cardinal points.

Botanical nomenclature follows Bailey *et al.* (1976) and Henderson (1997).

Terminology of cicadoid imago structures, for the most part, follows Kramer (1950) and Moulds (1990); wing venation is based on that of Dworakowska (1988) (Figs. 1, 2).

Terminology of male genitalia follows Orian (1964) for structures of the aedeagus while terminology for the pygofer is adapted from Duffels (1977, 1983) and Dugdale (1972) (Figs. 3–6). Two new structures, both apparently unique to the *Abricta* complex and associated with the aedeagus, are recognized here. A membranous transverse lobe positioned ventrally near the apex of the theca I call the flabellum (from the Latin meaning a fan, neuter) and a lightly sclerotized flap attached to the ventral side of the theca, proximal to the flabellum, I call the palearis (from the Latin for dewlap; neuter). The function of both these structures is unknown but they provide significant taxonomic characters at the species level.

#### Historical review

Abricta was erected by Stål (1866) as a subgenus of *Tibicen* Latreille to accommodate *Tettigonia brunnea* Fabricius, *Cicada tephrogaster* Boisduval and his new species *ferruginosus*. Three further species were added by subsequent authors before Karsch (1890) raised *Abricta* to generic rank, although the choice of *brunnea* as the type species for *Abricta* was made by Distant (1905a) who simultaneously described two additional species.

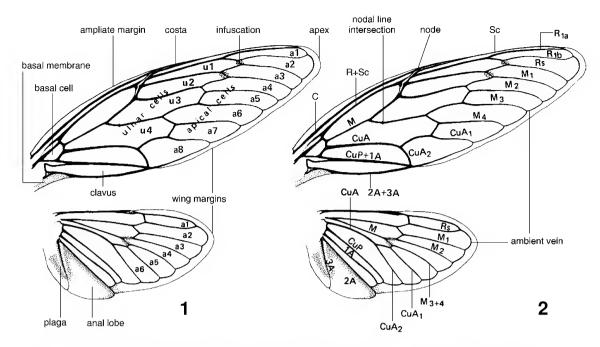
The first monograph of Australian cicadas (Goding & Froggatt, 1904) failed to recognize *Abricta* at generic rank, using Tibicen instead. Goding and Froggatt included a potpourri of 19 Australian species in Tibicen, of which eight were described as new. In 1906 W.L. Distant published his synonymic catalogue of cicadas (Distant, 1906), which corrected many wrong generic placements of previous authors, including a number of those introduced by Goding and Froggatt. Distant listed 12 species in Abricta (nine from Australia, two from Mauritius and one from Guatemala) plus six species he tentatively placed in Abricta. In his catalogue, under the heading "Synopsis of Genera" for his Division Taphuraria (p. 128), Distant provided a clear summary of Abricta characters, the first assessment of the taxon since Stål's original (and very brief) description. A partial review of genitalic structures of Abricta ferruginosa was later provided by Orian (1964), and Boulard (1979, 1990) has compared Abroma Stål and Abricta. There has been no further assessment of Abricta apart from a recent brief statement in Moulds (1990).

Z.P. Metcalf's (1963) catalogue of world Homoptera covered available literature to 1955 and listed 19 species of Abricta. Burns' (1957) checklist of Australian cicadas listed 14 Australian Abricta species, while Metcalf listed 13 from Australia. Burns had overlooked the transfer of hirsuta Goding & Froggatt to the genus Diemeniana Distant by Hardy (1918). Burns also listed the junior homonym aurata Walker instead of its replacement name euronotiana Kirkaldy. The year following publication of his checklist, Burns (1958) revised the genus Diemeniana and transferred Abricta euronotiana (having realized the homonymy of aurata) to the genus Diemeniana.

In 1962 Dlabola described a new species of *Abricta*, the first in 42 years. This fell, however, as a junior synonym of *Monomatapa insignis* Distant (Boulard, 1980).

Duffels & van der Laan (1985) listed 17 *Abricta* species, having eliminated *flava* Goding & Froggatt which Burns (1957) had included doubtfully in *Abricta*. The number of species in *Abricta* was further diminished by Boulard (1988) who transferred *flavoannulata* Distant to *Kanakia* Distant.

By 1990 16 species remained in *Abricta*. After examining the types of most Australian species, I concluded that another species, *frenchi* Distant, also belonged to *Diemeniana* and that *Abricta elseyi* Distant was a junior synonym of *Abricta rubra* (Goding & Froggatt). Thus 14 species remained in the genus (Moulds, 1990). However, at that time I was unable to assess the status of three further Australian *Abricta* species: *borealis* (Goding & Froggatt), *burgessi* Distant and *occidentalis* (Goding & Froggatt); nor did I assess non-Australian species then placed in *Abricta* apart from the type species, *brunnea* Fabricius.



Figs. 1–2. Simplified diagrams showing principal wing features of *Aleeta curvicosta*: (1) fore and hind wings showing wing areas and features; (2) fore and hind wings showing venation. Terminology adapted from Kukalová-Peck (1983), Boulard (1996) and Dworakowska (1988). A, anal vein; a, apical cell; C, costal vein; CuA, cubitus anterior vein; CuP, cubitus posterior vein; M, median vein; R, radius; Sc, subcostal vein; u, ulnar cell.

#### Species incorrectly assigned to Abricta

The following species do not fall within *Abricta* complex of genera and are excluded from this revision.

Tibicen borealis Goding & Froggatt, 1904, described from King George's Sound, Western Australia, was tentatively transferred to *Abricta* by Distant (1906). Syntype male in ANIC (ex MM) (Hahn, 1962; Stevens & Carver, 1986) (examined). This species clearly lacks characters of the *Abricta* complex and is to be placed in a new genus (Moulds, in prep.).

Abricta burgessi Distant, 1905, described from near Ingham, Queensland, has remained in Abricta since its description (Distant, 1905a). Syntype male in BMNH (examined). This species clearly lacks characters of the Abricta complex and will be so treated in a forthcoming work (Moulds, in prep.).

**Tettigonia cincta Fabricius**, **1803**, described from New Cambria (= Australia), was tentatively transferred to *Abricta* by Distant (1906). This species clearly lacks characters of the *Abricta* complex and will be treated in a forthcoming work (Moulds, in prep.).

*Tibicen occidentalis* Goding & Froggatt, 1904, described from Western Australia, was placed in *Abricta* by Distant (1906). Holotype male in ANIC (ex MM) (Hahn, 1962; Stevens & Carver, 1986) (examined). This species lacks characters of the *Abricta* complex and is to be placed in a new genus (Moulds, in prep.).

*Tettigonia pusilla* Fabricius, 1803, *nomen dubia* was tentatively transferred to *Abricta* by Distant (1906). Type female in UZMC (ex University of Kiel collection) (Zimsen, 1964) (examined). The specimen does not have a locality label—just a slip of paper with the word "*pusilla*", probably in Fabricius' handwriting.

Fabricius (1803) records this species from Amboina (= Ambon) in the Moluccas. J.P. Duffels & A.J. De Boer (pers. comm.) know Moluccan cicadas well and believe it does not come from the Moluccas. I am also certain it is not of Australian or New Zealand origin. Atkinson (1886) listed *pusilla* amongst "Species of doubtful position" recording it from Amboina and India. In the absence of any other Indian record and Atkinson's expression of doubt concerning its presence there, it seems reasonable to also dismiss India as a place of origin for this species.

The specimen clearly does not belong to *Abricta* or allied genera; the fore wing costa is not dilated and the build of the body is slender. At first glance it appears to belong to the Cicadettini but fore wing veins M and CuA remain unfused. Without an associated male it is impossible to determine its true identity or placement, and it is here treated as a *nomen dubia*.

# Cladistic analyses

**Outgroup choice**. Classification of the Cicadidae is still based, to a considerable degree, upon the arrangement proposed by Distant (1906). Generic relationships remain little understood and locating the sister groups of *Abricta* and its allied genera has been somewhat a hit-and-miss exercise. Boulard (1979, 1990) discussed the close

relationship of Abricta with Abroma Stål and suggested that they could even be synonymous; he also mentioned the similarity of Trismarcha Karsch with Abricta. Further, Boulard (1980) discussed the similarity of Monomatapa Distant to Abricta. Thus, Abroma, Monomatapa and Trismarcha were all considered as potential outgroups. However, examination of the type species of *Abroma*, *Abricta*, Monomatapa and Trismarcha showed closest similarities between Monomatapa, Abroma and Abricta; Trismarcha was much less similar. For this reason *T. umbrosa* Karsch (Fig. 39) (the type species of *Trismarcha*) was chosen as the outgroup and Monomatapa insignis Distant and Abroma guerinii (Signoret) (also type species of their genera) were incorporated as part of the ingroup. Additional species of Abroma, Monomatapa and Trismarcha were omitted because of uncertainties of their generic placements.

Characters. From a detailed study of morphology 24 characters were selected for use in the cladistic analyses. Fourteen characters are binary and ten 3-tier multistate. Morphology, apart from male genitalia, showed comparatively few differences among the species under study. Over half the characters, 13 of the 24, were obtained from male genital structures. Female genitalia showed only one character sufficiently different among species to provide useful data. The characters and character states used were as follows.

#### Head

Character 1: Head width/anterior pronotum width ratio

- (0) > 1.1
- (1) 0.9-1.1
- (2) < 0.9

Character 2: Eye size

- (0) average (distance between them much greater than half total head width)
- (1) large (distance between them half or less of total head width)

#### Thorax

Character 3: Pronotum to mesonotum colour

- (0) unicolorous
- (1) bicolorous

# Male opercula

Character 4: Male opercula

- (0) meeting or very nearly meeting
- (1) clearly separated

#### **Tymbals**

Character 5: Number of tymbal ridges

- (0) 8 (Figs. 8, 21)
- (1) 9-14 (Figs. 19, 20, 22-29)

# Wings

Character 6: Fore wing costa

- (0) weakly dilated
- (1) strongly dilated to node

Character 7: Fore wing anal angle

- (0) clearly defined; wing margin strongly bent at apical cell 8
- (1) ill defined; wing margin nearly straight at apical cell 8

Character 8: Fore wing infuscation

- (0) absent or present on bases of apical cells 2 and 3
- (1) continuous along bases of apical cells 2-4

#### Abdomen

Character 9: Width of male abdomen

- (0) broader than thorax
- (1) equal to thorax

Character 10: Abdominal pubescence

- (0) golden
- (1) silver

# Male genitalia

Character 11: Upper pygofer lobe length

- (0) very short
- (1) much shorter than dorsal beak
- (2) equal to or longer than dorsal beak

Character 12: Upper pygofer lobe apex

- (0) rounded
- (1) straight and pointed
- (2) upturned and pointed

Character 13: Secondary upper pygofer lobe

- (0) absent
- (1) present

Character 14: Basal pygofer lobe

- (0) small and rounded
- (1) bluntly pointed and webbed
- (2) bluntly pointed and finger-like

Character 15: Secondary basal pygofer lobe

- (0) absent
- (1) present

Character 16: Distal end of uncal lobe

- (0) downturned
- (1) upturned

Character 17: Uncal lobe shape

- (0) claw-like (Fig. 32)
- (1) disc-like (Fig. 6)
- (2) scoop-like (Fig. 4)

Character 18: Uncal lateral process

- (0) absent
- (1) short and rounded
- (2) linear and nearly equal in length to upper pygofer lobe

Character 19: Palearis

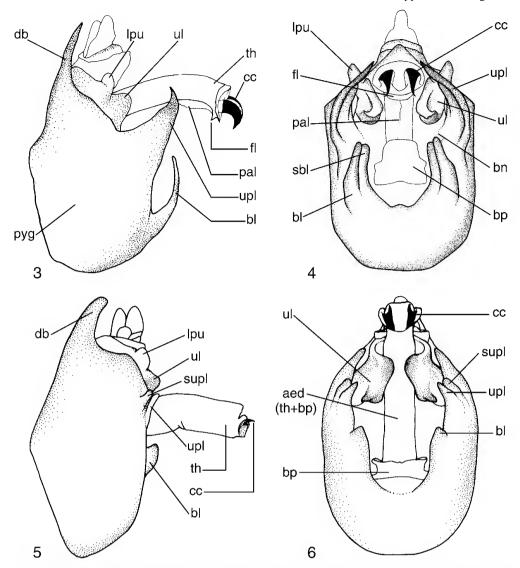
- (0) absent
- (1) small and lobe like
- linear and extending at least one quarter length of theca

Character 20: Flabellum

- (0) absent
- (1) small and bilobed
- (2) expanded, ovate

Character 21: Conjunctival claw development

- (0) absent
- (1) robust, claw-like with no associated sclerotization (Figs. 3, 4)



Figs. 3–6. Male genitalia of *Tryella ochra* (3,4) and *Abroma guerinii* (5, 6); lateral views at top, ventral views at bottom. Terminology after Duffels (1977), Dugdale [1972] and Orian (1964). Abbreviations: *aed*, aedeagus; *bl*, basal lobe of pygofer; *bn*, basal knob of median rib of upper pygofer lobe; *bp*, basal plate; *cc*, conjunctival claw; *db*, dorsal beak; *fl*, flabellum; *lpu*, lateral process of uncus; *pal*, palearis; *pyg*, pygofer; *sbl*, secondary basal lobe of pygofer; *sulp*, secondary upper pygofer lobe; *th*, theca; *ul*, uncal lobe; *upl*, upper lobe of pygofer.

(2) fused with, or adjoining, a basolateral sclerotization (Figs. 5, 6)

Character 22: Conjunctival claw orientation

- (0) ventral
- (1) lateral

Character 23: Conjunctival claw apex

- (0) simple
- (1) complex

# Female genitalia

Character 24: Ovipositor apex in lateral view

- (0) short, rounded (Fig. 7)
- (1) long, with strong dorsal downward slope (Fig. 8)
- (2) long, with modest ventral and dorsal slopes (wedge shaped) (Figs. 9–14)

#### **Discussion of characters**

**Head**. The species of the *Abricta* complex of genera all possess a broad head compared to most other cicadas and a postclypeus that is only weakly convex at its anterior margin so that it is almost continuous with the anterior margins of the vertex lobes. This is so even for *Tryella crassa* n.sp. and *T. graminea* n.sp., which are the only species in which the head is narrower than the anterior pronotum (character state 1.2). The head width of all other Australian species of the *Abricta* complex is about equal to that of the anterior pronotum (1.1) while the head is distinctly wider in all non-Australian taxa (1.0).

The Afrotropical *Abricta* and *Abroma* species possess enlarged eyes which tend to dominate the head (character state 2.1), while other Australian species of the *Abricta* complex of genera have eyes of more or less normal size (2.0). The rostrum length of all species is remarkably similar, reaching to somewhere between the distal ends of the mid and hind coxae. Head colour is either black, brown or more

often a combination of both. Both rostrum length and head colour have been considered unsuitable characters for inclusion in the cladistic analysis because they lack definable states.

**Thorax**. Thoracic morphology shows little diversity throughout the *Abricta* complex of genera. The pronotal collar is depressed and fused laterally although the rounded lateral angles are moderately developed.

Colour tonal contrast between the pronotum and mesonotum is a reasonably stable diagnostic character (character 3). The Neotropical species *Chrysolasia guatemalena* has a unicolorous thorax, along with five Australian species. All of the Afrotropical species examined, *Monomatapa insignis, Abricta brunnea, A. ferruginosa* and *Abroma guerinii*, plus the remaining ten species of the *Abricta* complex from Australia, are bicolorous with the pronotum paler than the mesonotum. Only *Tryella stalkeri* was found to include some individuals tending unicolorous rather than bicolorous. Other colour patterns and colours were found to be too inconsistent within species and were not used in the cladistic analysis.

Male opercula. The opercula of *Abricta* and allied genera are nearly flat, distally rounded plates that cover the tympanal cavities. For the most part they are confined within, or just beyond, the limits of the tympanal cavities; only in *Aleeta curvicosta* do they extend noticeably beyond, both distally and laterally. Moderate differences in size are reflected by the opercula either meeting or not meeting (character 4). Opercula colour ranges from muddy pale yellow to black but the considerable range of variation encountered in most species excludes opercula colour from being a satisfactory diagnostic character.

Male tymbals. Tymbal morphology throughout Abricta and its allied genera is very similar. A series of long, nearly parallel ribs dominate the tymbal and the basal plate is always small (Figs. 18-29). The number of ribs varies between species from 8 to 14 (character 5). Conspecific deviation by one or two ribs is sometimes encountered in some species. The Afrotropical species, Abricta brunnea, A. ferruginosa and Abroma guerinii, normally have 10–14 ribs (Fig. 19), the Australian Aleeta curvicosta normally has 12 (Fig. 20) while the Australian Tryella species and the African *Monomatapa insignis* have 9–11 (usually 10) (Figs. 22–29) and the Neotropical Chrysolasia guatemalena 8 (Fig. 21). The outgroup taxon Trismarcha umbrosa from Africa also has 8 (Fig. 18). Because of the variation encountered in the number of ribs within Abricta, Abroma, Aleeta and Tryella, scoring of these genera has been categorized as 9 or more ribs.

Wings. Wing morphology is similar to that found in many other cicadas. Two useful morphological characters have been identified for *Abricta* and its allied genera. The fore wing costa (character 6) shows marked dilation in all Australian species (6.1). There is also a tendency for other species of the *Abricta* complex of genera to show fore wing costal dilation but it is minimal compared with that of Australian species. Fore wing shape (character 7) of Australian species of the *Abricta* complex also differs from non-Australian species of the complex; the anal angle of Australian species complex being substantially lost (7.1).

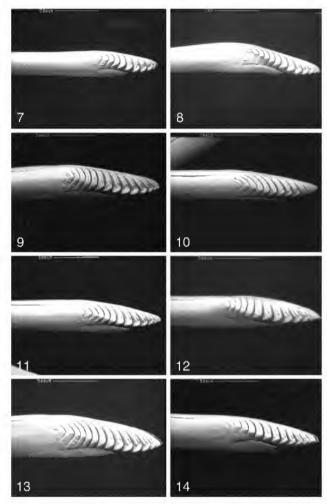
Fore wing infuscation (character 8) varies considerably, both between species and within some species. The most extensive infuscation, continuous along the bases of apical cells 2–4 (8.1), is found in Tryella noctua (Distant), T. occidens n.sp. and T. stalkeri (Distant) from Western Australia plus T. infuscata n.sp. from the Northern Territory and northwestern Queensland. Such infuscation is always present between apical cells 2–4. Three other Tryella species, T. kauma n.sp., T. ochra n.sp. and T. lachlani n.sp., all from Queensland, plus all non-Australian species of the *Abricta* complex of genera, totally lack fore wing infuscation. The eight remaining species (all from Australia) have infuscation that is confined to the bases of apical cells 2 and 3 only. However, the extent of this infuscation is highly variable in most of these species; the majority of individuals have an infuscation that is subdivided, some have continuous infuscation and some individuals of some species lack infuscation altogether. While this range of variation is evident in all species, extremes are uncommon except in Tryella castanea Distant. Because of the variable nature of infuscations in these species a distinction has not been made between the presence of these small infuscations and their absence.

Male abdomen. The width of the male abdomen (character 9) is equal to that of the thorax (9.1) in all species except *Chrysolasia guatemalena* and *Monomatapa insignis*. Overall abdominal shape is similar for most species with the basal segments showing minimal taper.

Distinct pubescence on the abdomen (and often also on head, thorax, legs and basal wing veins) (character 10) is a typical feature of all species of the Abricta complex. The Australian species all carry a very fine "powder-like" silver pubescence, especially Aleeta curvicosta, Tryella rubra, T. occidens and T. noctua (10.1). However, this pubescence is often partly or entirely abraded. Abricta brunnea and A. ferruginosa from Mauritius plus Abroma species appear to carry similar pubescence but it was not obvious on those specimens I have examined, probably because all have been old and worn. By contrast, Chrysolasia guatemalena has prominent pubescence which is clearly hair-like and is not easily abraded, and is of a distinct golden colour on the abdomen (10.0). The outgroup taxon, Trismarcha umbrosa, is the only other species under study that possesses such golden pubescence.

Male genitalia. The upper pygofer lobes show considerable specific differences both in size and shape (character 11). In their extremes they are either very short as in the Afrotropical Abricta brunnea, A. ferruginosa, Abroma guerinii and Monomatapa insignis plus the Neotropical Chrysolasia guatemalena (11.0), or strongly developed as in all Australian species of the Abricta complex (11.2) except Aleeta curvicosta and Tryella occidens (11.1). The distal ends of these structures (character 12) are either rounded as in most Australian species and the Abricta species, Abroma guerinii and Monomatapa insignis (12.0), straight and pointed as in *Chrysolasia guatemalena* (12.1), or upturned and pointed as in the remaining Australian species of the Abricta complex (12.2). These states of character 12 only in part support monophyletic groupings but are important diagnostic tools at the species level.

Secondary upper pygofer lobes (character 13) are restricted to the Afrotropical species *Abricta brunnea, A. ferruginosa* and *Abroma guerinii*.



Figs. 7–14. Distal end of female ovipositor in lateral view: (7) *Trismarcha umbrosa*, Boukoko, Republic of Central Africa; (8) *Aleeta curvicosta*, Kuranda, northern Qld; (9) *Tryella burnsi*, Kuranda, northern Qld; (10) *T. castanea*, Waterhouse R., NT; (11) *T. kauma*, East Haydon, northern Qld; (12) *T. lachlani*, "York Downs", northern Qld; (13) *T. rubra*, Waterhouse R., NT; (14) *T. stalkeri*, De Grey R., WA.

The basal pygofer lobes (character 14) show three distinct states, considered most derived when finger-like in seven of the 15 Australian species of the *Abricta* complex (14.2). This lobe is small and rounded (14.0) in the Mauritian species *Abricta brunnea* and *A. ferruginosa*, while it is distinctly webbed (14.1) in the Afrotropical *Abroma guerinii* and *Monomatapa insignis*, the Neotropical *Chrysolasia guatemalena*, and the remaining Australian species of the *Abricta* complex. The development of these lobes in part supports monophyletic groupings and is also an important diagnostic character at species level.

The secondary basal lobes of the pygofer (character 15) are present in all Australian species of the *Abricta* complex and the Neotropical species *Chrysolasia guatemalena* (15.1) but absent from all Afrotropical species studied (15.0).

The shape of the uncal lobes is diverse and provides useful diagnostic characters. The distal ends of the uncal lobes are either downturned as in all the Afrotropical species studied plus the Australian *Aleeta curvicosta*, or upturned as in all *Tryella* species (character 16). Overall shape falls into three distinct categories; claw-like (Fig. 47) as in *Aleeta* 

curvicosta and the outgroup *Trismarcha umbrosa*, disc-like (Fig. 6) as in *Abricta* species, *Abroma guerinii*, *Chrysolasia guatemalena* and *Monomatapa insignis*, and scoop-like (Fig. 4) as in all species of the Australian genus *Tryella* (character 17).

The uncal lateral processes (character 18) are absent in all Afrotropical species studied and also the Australian species *Aleeta curvicosta*. Intermediate development, in which the processes are short and rounded, occurs five of the Australian *Tryella* species, while linear development is found in the remaining nine Australian *Tryella* species.

A palearis (character 19) occurs in eight of the Australian *Tryella* species but is otherwise unknown in Cicadoidea. In four of these species, *graminea*, *occidens*, *stalkeri* and *willsi* it is small and lobe-like (19.1) but in *infuscata*, *lachlani*, *noctua* and *ochra* it is clearly linear (19.2).

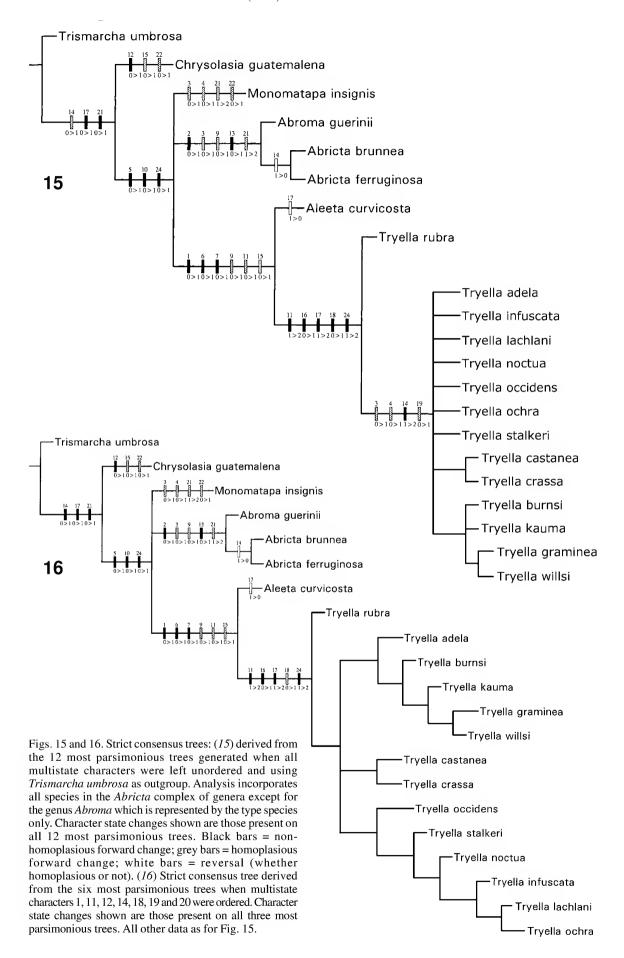
A flabellum (character 20) is found in five Australian *Tryella* species and, like the palearis, is otherwise unknown in Cicadoidea. This membranous structure occurs either as a bilobed flange as in *adela* and *burnsi* (20.1), or as a large ovate flange as in *graminea*, *kauma* and *willsi* (20.2).

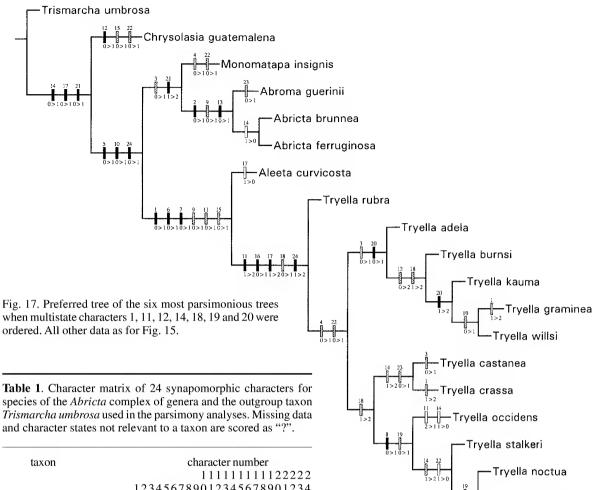
The conjunctival claws are unique to Abricta and allied genera. These paired structures show varying degrees of development, orientation and ornamentation, and are useful diagnostic characters both at generic and species levels. Claw development (character 21) falls into two primary groupings; all Australian species of the *Abricta* complex and Chrysolasia guatemalena have robust, cat-like claws with no associated sclerotization (21.1) while the Afrotropical Monomatapa insignis, Abricta brunnea, A. ferruginosa and Abroma guerinii have smaller claws that are associated with a basolateral sclerotization (21.2). Of those species with state 21.1, Tryella occidens, Aleeta curvicosta and Chrysolasia guatemalena, have claws that differ in their detailed structure. Tryella occidens has broad, dorsally excavated claws. Aleeta curvicosta and Chrysolasia guatemalena have claws of a more slender build but which differ significantly from each other in shape, those of curvicosta being somewhat flattened laterally, those of guatemalena tending to be tubular. These autapomorphies help delineate the genera Chrysolasia and Aleeta. Claw orientation (character 22) delineates two distinct groupings, those with claws directed either laterally or ventrally. This distinction is clear-cut except for Tryella occidens in which the claws are lateral but with a slight upward trend and for Chrysolasia guatemalena where the claws are lateral but with a downward trend. The apices of the conjunctival claws (character 23) show complex toothing in Tryella castanea and T. crassa but in all other species of the Abricta complex they terminate in a simple point.

**Female genitalia**. Female genital structures showed only one character displaying discernible synapomorphies. Small differences were detected in the apical shape of the ovipositor in lateral view (character 24) (Figs. 7–14).

# Computation

The coded character state data given in Table 1 were analysed using the microcomputer programs Hennig86 (version 1.5, Farris, 1989) and PAUP\* (version 4.0b10, Swofford, 2000). Employing Hennig86, trees were computed using options m\* and bb\*. Using PAUP\*, a heuristic search was applied. Data were run both with





taxon	character number	
	111111111122222	
	123456789012345678901234	
Trismarcha umbrosa	000000000000000000000000000000000000000	
Monomatapa insignis	001110000100010010002101	
Abroma guerinii	011010001100110010002001	
Abricta brunnea	011010001100100010002001	
Abricta ferruginosa	011010001100100010002001	
Chrysolasia guatemalena	0000000000101101000110?	
Aleeta curvicosta	100011101110011000001001	
Tryella adela	101111101120011121011102	
Tryella burnsi	101111101122011122011102	
Tryella castanea	101111101120021122001112	
Tryella crassa	200111101120021122001112	
Tryella graminea	201111101122011122121102	
Tryella infuscata	101111111120021121201002	
Tryella kauma	101111101122011122021102	
Tryella lachlani	101111101120021121201002	
Tryella noctua	100111111120021122201002	
Tryella occidens	1001111111110001122101102	
Tryella ochra	101111101122021121201002	
Tryella rubra	100011101120011121001002	
Tryella stalkeri	10?111111120021122101002	
Tryella willsi	101111101122011122121102	

multistate characters unordered and with characters 2, 11, 12, 14, 18, 19 and 20 ordered. Weighting of characters was not employed. To identify common elements among the equally most parsimonious trees found, consensus trees were computed using the Nelsen option of Hennig86 and the strict consensus option of PAUP\*.

Tree files generated from Hennig86 were analysed using CLADOS (version 1.2, Nixon, 1992). Characters were

optimized using the default setting, which favours reversals over parallel developments (ACCTRAN). Rooting of trees to the outgroup from the basal default trichotomy of Hennig86 was achieved using the Move option of CLADOS.

Tryella infuscata

vella ochra

# Results and discussion

Processing of the data, using Hennig86 and PAUP\*, produced 12 most parsimonious trees of length 53 steps, a CI of 64 and a RI of 82, when all multistate characters were left unordered and autapomorphies excluded. Consensus trees from Hennig86 and PAUP\* (applying the strict consensus option) were identical. These consensus trees were fully resolved except for a trichotomy made up of Monomatapa insignis, a clade comprising Abricta and Abroma species, and a clade comprising all Australian species which itself was mostly unresolved (Fig. 15). Rerunning the data with multistate characters 1, 11, 12, 14, 18, 19 and 20 ordered gave six trees of length 56, CI 60 and RI 83. A strict consensus tree showed the clade of Australian species almost entirely resolved (in marked contrast to the tree resulting from unordered characters), while the non-Australian taxa remained resolved exactly

as when all multistate characters were left unordered (Fig. 16). Thus, resolution among the Australian species of the *Abricta* complex is dependent upon the hypothesis of the character ordering used while placement of all non-Australian taxa is unchanged whether characters are ordered or not.

The analyses placed *Chrysolasia guatemalena* (from South America) as the sister group of all other species of the *Abricta* complex of genera. These other species were united by three non-homoplasious synapomorphies (characters 5, 10 and 24) and in turn were divided into a trichotomy of two African clades and a clade of Australian species. In the preferred tree resulting from when characters were ordered (Fig. 17) the African species are a monophyletic group supported by one non-homoplasious synapomorphy (21.2) and one homoplasious synapomorphy (3.1). The Australian clade was supported by three non-homoplasious synapomorphies (1.1, 6.1 and 7.1) and three homoplasious synapomorphies (9.1, 11.1 and 15.1).

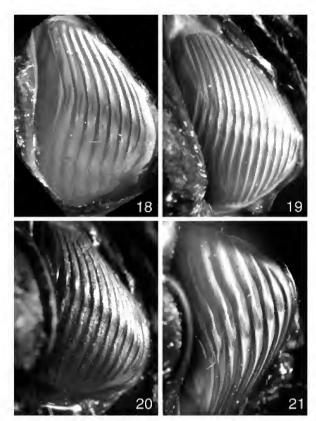
Within the Australian clade, *Aleeta curvicosta* formed a sister group to all remaining species. The sister group of *curvicosta* was strongly supported by four non-homoplasious synapomorphies (11.2, 16.1, 17.2 and 24.2) and one homoplasious synapomorphy (18.1).

Among the 14 species making up the sister group of curvicosta (the genus Tryella) four groupings were identified: rubra as the sister group of all others (so placed in all analyses done, Figs. 15–17); the occidens species group containing occidens, stalkeri, noctua, infuscata, ochra and lachlani; the adela species group containing adela, burnsi, kauma, graminea and willsi, and a clade comprising castanea and crassa that is weakly associated with the adela group. Apart from rubra, none of these groupings are strongly supported although they do show relationships that follow logical geographic patterns as discussed below.

#### Rationale for new taxa

# Chrysolasia n.gen.

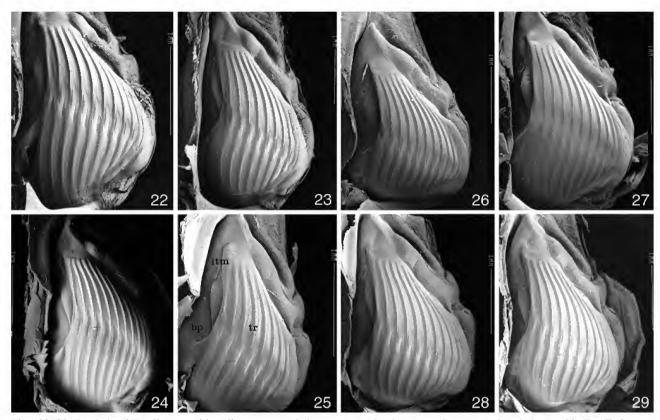
The single Central American species, *Abricta guatemalena*, is phylogenetically distant from other Central American cicadas (J. & M. Heath, pers. comm.) and geographically isolated from other species of the *Abricta* complex of genera, i.e. the Afrotropical Abricta/Abroma/Monomatapa species and the Australian species. This geographic separation is reflected in the cladistic analyses by its sister-group relationship with all other species of the Abricta group. Three apomorphies support the distinctive nature of guatemalena, one non-homoplasious synapomorphies (12.1) and two homoplasious forward changes (15.1 and 22.1) (Figs. 15-17). Further, three non-homoplasious characters (5.1, 10.1 and 24.1) differentiate the sister clade of guatemalena. These well supported nodes, in addition to three further autapomorphies for guatemalena (golden, hair-like pubescence on the body, apex of upper pygofer lobes straight and pointed, nodal line intersection near midpoint of ulnar cell, and eight tymbal ridges) are considered to provide sufficient justification for the generic separation of *guatemalena* from other species of the complex.



Figs. 18–21. Tymbals of *Trismarcha*, *Abricta*, *Aleeta* and *Chrysolasia* species. (18) *Trismarcha umbrosa*, Boukoko, Republic of Central Africa; (19) *Abricta brunnea*, Mauritius; (20) *Aleeta curvicosta*, Kuranda, northern Qld; (21) *Chrysolasia guatemalena*, Purula, Guatemala.

#### Abricta s.str.

In the cladistic analyses, the preferred tree (Fig. 17) shows that the Afrotropical Abricta/Abroma clade is supported by two non-homoplasious synapomorphies (2.1 and 13.1) and one homoplasious forward change (9.1). The sister clade of Abricta/Abroma in the preferred tree (Fig. 17), comprising the Afrotropical monotypic genus Monomatapa, is characterized by two homoplasious forward changes (4.1 and 22.1). Monomatapa insignis is also differentiated from Abricta and Abroma by three autapomorphies, its broad male abdomen, linear and tear-drop shaped male opercula and the double-pointed apices of the uncal lobes. All these apomorphies support the generic separation of Abricta and Abroma from Monomatapa. Further, there is clear separation of Abricta, Abroma and Monomatapa from all Australian species of the *Abricta* complex as discussed in Results above. The separation of *Abricta* from *Abroma* is supported by just one homoplasious reversal (14.0). Abroma guerinii also differs from Abricta by having the conjunctival claws apically bifurcate rather than simple. Both these attributes are relatively minor points of difference and the possible synonymy of Abricta and Abroma, as suggested by Boulard (1979, 1990), is supported by this evidence. However, synonymy has not been pursued here as a study of all Abroma species was not possible. The restriction of Abricta as defined here to just two Mauritian species, requires that the Australian species (all of which have been previously placed in Abricta) be placed elsewhere.



Figs. 22–29. Tymbals of *Tryella* spp. with rudimentary tymbal covers completely removed to expose basal plates: (22) *Tryella burnsi*, Townsville, northern Qld; (23) *Tryella crassa*, Cloncurry, northern Qld; (24) *Tryella graminea*, Torrens Creek township, northern Qld; (25) *Tryella kauma*, East Haydon, northern Qld. (26) *T. noctua*, Marla, SA; (27) *T. ochra*, Walker Ck, northern Qld; (28) *T. rubra*, Waterhouse R., NT; (29) *T. stalkeri*, De Grey R., WA. Abbreviations: *bp*, basal plate; *itm*, insertion of tymbal muscle; *tr*, tymbal rib.

#### Aleeta n.gen. and Tryella n.gen.

Within the Australian clade the strong differentiation between curvicosta and all other Australian species (Figs. 15-17) supports the generic separation of *curvicosta*. This generic separation is further supported by six autapomorphies: male genitalia with beak-like uncal lobes, partially bifurcate upper pygofer lobes, a pair of sublateral flanges near the distal end of the theca and laterally flattened conjunctival claws, plus male opercula that extend clearly beyond the lateral margins of the abdomen. It is proposed here that *curvicosta* be placed in the monotypic genus Aleeta n.gen. The sister clade of curvicosta, to be proposed here as the genus Tryella n.gen., is well supported by four non-homoplasious synapomorphies (11.2, 16.1, 17.2 and 24.2) and one homoplasious forward change (18.1). The generic separation of Aleeta and Tryella is also supported by electrophoretic analyses which revealed a great genetic distance between Aleeta curvicosta and five Tryella species that were available for study (Serkowski & Moulds, unpub. data).

#### Tryella species

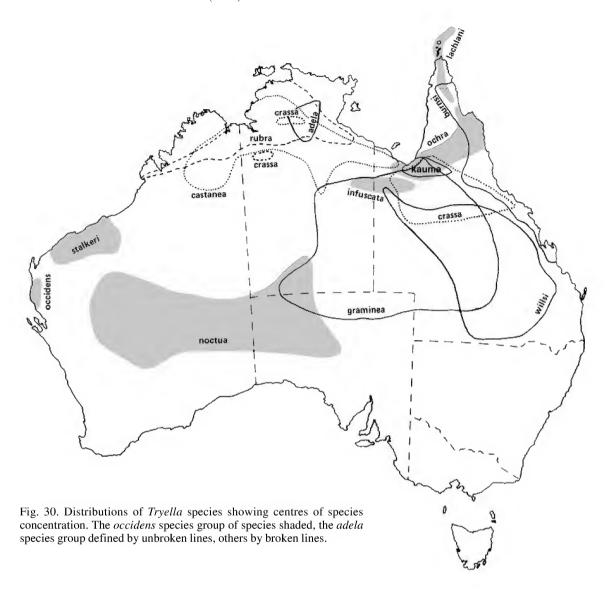
Electrophoretic analyses grouped populations of *Tryella* species in a way that was consistent with different male genitalic morphologies (Serkowski & Moulds, unpub. data). Colour, colour pattern and size were not always consistent within these species groupings suggesting that these features are not necessarily reliable indicators of species limits. Male genitalic morphologies did, however, correlate with

differences in wing and body morphologies (apart from size) where differences could be discerned. Thus, differences in male genitalic morphology have been given considerable emphasis in delineating *Tryella* species. While the converse is not necessarily true, i.e. individuals with identical male genitalia may not be conspecific, there was no evidence from either electrophoretic data or song analyses (Moulds, unpub. data) suggesting that this might be so.

# Biogeography

**Distribution of** *Abricta* **and allied genera**. The six genera of the *Abricta* complex fall into distinct geographic regions. *Abricta* sensu str. and *Monomatapa* are strictly Afrotropical in distribution. *Abroma* has an Afrotropical type species but is otherwise widely distributed through Mauritius, Madagascar, Sri Lanka, and possibly India, and doubtfully through southeast Asia, and even South America; special caution should be exercised in including those species of non-Afrotropical origin in *Abroma* as none have been adequately described and further examination is likely to show that some at least do not belong to *Abroma*.

Aleeta and Tryella are restricted to Australasia. The sole representative of Aleeta, A. curvicosta, is endemic to eastern Australia. The 14 known Tryella species are also endemic to Australia, except for T. lachlani that marginally extends its distribution to the southwest coast of Papua New Guinea. Only two Tryella species have distributions that partly impinge on that of Aleeta. The distribution of Chrysolasia remains uncertain.



**Distribution of** *Tryella* **species** (Fig. 30). *Tryella* species occur primarily across the northern half of Australia with just two extending south of 30°S latitude. Most have extensive distributions spanning at least 500 km. The apparent absence of *Tryella* species from Arnhem Land and the Tanami Desert regions of the Northern Territory, and the Kimberley and Pilbara regions of Western Australia is most likely a consequence of insufficient collecting.

The occidens species group, comprising occidens, stalkeri, noctua, infuscata, ochra and lachlani, has a distribution that extends from Western Australia northeastwards to Cape York Peninsula. There is a direct correlation between the distribution of these species and their phylogenetic positions from the cladistic analyses (Fig. 17), with the most ancestral species occurring in the far west of Western Australia and the most derived in the north of Cape York Peninsula. The disjunct distributions of the three Western Australian species suggest that they were once far more widespread and have contracted their ranges with changing habitat.

The adela species group comprising adela, burnsi, kauma, graminea and willsi, and the possibly allied species

castanea and crassa, is widespread across the monsoonal north of Western Australia, the Northern Territory and Queensland; only graminea and willsi extend their ranges beyond the monsoonal north to reach the drier interior of the northeast quarter of Australia.

The sister group relationship of rubra with the adela species group and its allies castanea and crassa also reflects a western (or northwestern) origin for Tryella. The distribution of rubra is consolidated across the western limits of the adela species group, that is, across the distributions of castanea, crassa and adela. These three species could be interpreted as the three basal taxa of the adela species group clade. This distribution pattern supports the hypothesis that the origin of the adela group was also somewhere in the west or north-west of the continent and radiated eastward into Queensland, rather than at the base of the Gulf of Carpentaria where the current concentration of species is found. The concentration of species at the base of the Gulf of Carpentaria could be a consequence of the eastward radiations of the occidens species group and adela species group converging.

# **Taxonomy**

# Abricta complex of genera

Five genera are here considered to belong to the *Abricta* complex of genera, viz. *Abricta* Stål sensu str., *Abroma* Stål, *Aleeta* n.gen., *Tryella* n.gen., *Chrysolasia* n.gen. and *Monomatapa* Distant. These genera are characterized by the conjunctival claws at the distal end of the male theca, and a partially or strongly dilated fore wing costa. On the basis of their type species, *Abricta* and *Abroma* should probably be synonymized, a decision not formally adopted here as an assessment of the 18 species of *Abroma* lies beyond the scope of this revision.

# Key to genera

1	
1	Anterior margin of fore wing strongly dilated proximal of node, the maximum dilation greater than width of costal vein (Fig. 55b)
	(Australian species)
	- Anterior margin of fore wing with dilation less than width of costal
	vein (Fig. 41b) (non-Australian species)
2	Fore wing rarely less than 32 mm long, usually more than 40 mm;
	male genitalia with uncal lobes downturned at their distal ends
	(Figs. 46, 47) (monotypic)
	- Fore wing never reaching 32 mm, usually less than 26 mm; uncal
	lobes upturned at their distal ends (Figs. 100, 101) (14 species)
3	Abdaman bassing distinct golden nubassansa, mala ganitalia with
3	Abdomen bearing distinct golden pubescence; male genitalia with conjunctival claws well developed and strongly recurved (Figs.
	35, 36) (monotypic, reputedly from Guatemala)
	- Abdomen bearing silver-white or no pubescence; male genitalia with conjunctival claws small, gently curved in an arc (Figs. 33,
	34, 37–38, 42–45)
	31, 37 30, 12 13)
4	Male abdomen much broader than thorax; male genitalia with
	conjunctival claws laterally directed (Figs. 33, 34)
	- Male abdomen as wide as thorax; male genitalia with conjunctival
	claws ventrally directed (Figs. 37–38, 42–45)
5	Mala with upper process labor poor tries are on the pay abounts
3	Male with upper pygofer lobes near triangular with apex sharply pointed in lateral view (Figs. 37, 38, 42, 43) (2 species, Mauritius
	& Reunion)
	- Male with upper pygofer lobes small, tending linear, apically
	rounded in lateral view (Figs. 44–45) (18+ species, Mauritius,
	Madagascar, Sri Lanka, India, and doubtfully Asia, South America,
	Philippines)
	rr

# Genus Abricta Stål, 1866

Tibicen (Abricta) Stål, 1866: 26; Dallas, 1867: 556; Atkinson, 1886: 187; Karsch, 1890: 116; Distant, 1892a: 127 (error); Schulze *et al.*, 1926: 4.

Abricta.—Karsch, 1890: 86, 108, 111; Karsch, 1891: 348; Karsch, 1893: 13; Kirkaldy, 1904: 282; Distant, 1905a: 27; Kuhlgatz, 1905: 78—80; Distant, 1906: 130; Froggatt, 1907: 351; Ashton, 1912: 24; Ashton, 1914: 349; Hardy, 1918: 70; Distant, 1920: 456; Delétang, 1923: 629; Handlirsch, 1925: 1116; China, 1929: 426, 427; Kato, 1932: 179, 181; Neave, 1939: 5; Orian, 1954: 235, 236; Tillyard, 1926: 161; Kato, 1956: 62, 69, 84; Dlabola, 1971: 151; Dugdale, 1972: 857; Young, 1973: 378; Fleming, 1975: 300; Popov, 1975a: 34; Popov, 1975b: 288; Richards & Davies, 1977: 184; Simmons & Young, 1978: 43; Boulard, 1979: 31, 33; Duffels & van der Laan, 1985: 233; Moulds, 1990: 118; Moulds & Carver, 1991: 467; Ewart, 1993: 139, 140; Zborowski & Storey, 1995: 87.

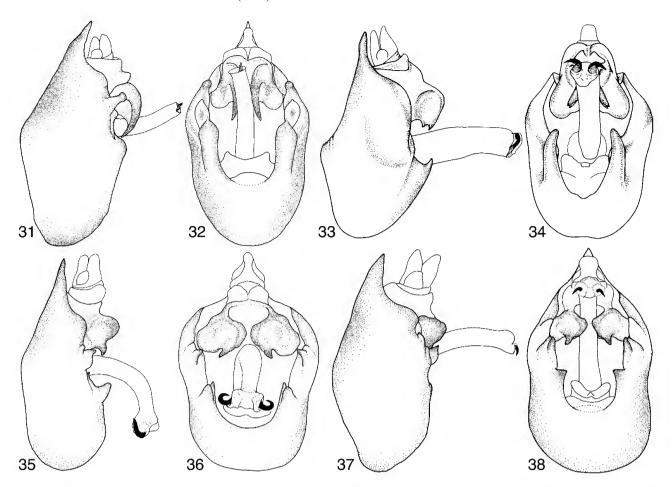
**Type species**. *Tettigonia brunnea* Fabricius, 1798 (type by subsequent designation).

Stål (1866) included three species in *Abricta (brunnea, ferruginosa* and *tephrogaster*, the latter in a footnote) without

selecting one as type species. Distant (1905a) was the first to do so, selecting *brunnea*. Under Article 69.1 of the *Code* Distant's designation fixes *brunnea* as type species.

**Included species**. In its present concept the genus *Abricta* contains only two species: *brunnea* Fabricius and *ferruginosa* Stål.

Diagnosis. Postclypeus slightly to moderately produced. Rostrum almost reaching or slightly passing hind coxae. Eyes large, their long axes together comprising approximately half total width of head. Width of head including eyes greater than width of anterior pronotum and nearly equal to width of mesonotum; width of male abdomen about equal to width of thorax. Pronotal collar narrow with lateral angles ampliate and rounded; rudimentary and essentially confluent with adjoining sclerites anterior of lateral angles. Wings hyaline or with weak translucent tint; without infuscations. Fore wing costal margin weakly ampliate to node, the maximum dilation less than width of costal vein; basal cell usually with translucent pigmentation, hyaline in some individuals. Hind wing plaga broad along vein 3A



Figs. 31–38. Male genitalia of *Trismarcha, Monomatapa, Chrysolasia* and *Abricta* species showing pygofer with uncus and aedeagus in right lateral view (left) and ventral view (right): (31–32) *Trismarcha umbrosa*, Boukoko, Republic of Central Africa; (33–34) *Monomatapa insignis*, Chiredzi, Zimbabwe; (35–36) *Chrysolasia guatemalena*, Purula, Guatemala; (37–38) *Abricta brunnea*, Mauritius.

and inner margin of anal lobe but never reaching distal end of 3A, absent or barely present along 2A. Tymbals with 11–14 long ribs evenly spaced and slightly converging dorsally; basal plate small (Fig. 19). Male opercula almost tear-drop in shape, weakly angled inwards before midpoint; nearly flat; meeting but not overlapping and extending distally to margin of tympanal cavities. Body and basal fore wing veins with some silver pubescence, probably extensive on newly emerged individuals.

Male genitalia (Figs. 37, 38, 42, 43) with pygofer dorsal beak large, long and pointed; upper pygofer lobes well developed, pointed and highly sclerotized, lacking setae; secondary upper pygofer lobes rounded, bearing long setae; pygofer basal lobes undivided, moderately developed, triangular in ventral view, bearing long setae. Uncal lobes disc-like, tending towards meeting but never doing so, each terminating in a thick-set, down-turned, blunt projection; uncal lateral processes absent. Aedeagus in lateral view straight or gently curved for most of its length but strongly recurved near base, basal plate a fused pair of nearly circular discs; conjunctival claws directed ventrally, simple, arising from inner surface of a large lateral basal flange; flabellum and palearis absent.

Female abdominal segment 9 very long, clearly more than half as long as abdominal remainder, nearly conical; ovipositor sheath terminating beyond distal end of dorsal beak.

**Distinguishing features**. The disc-like male uncal lobes combined with the reduced conjunctival claws clearly

separate Abricta and Abroma from Tryella n.gen., Aleeta n.gen. and Chrysolasia n.gen. Further, the weak ampliation of the fore wing costa of Abricta and Abroma immediately distinguishes these genera from Aleeta and Tryella in which the maximum ampliation at least equals the width of the costal vein. Abricta and Abroma are readily distinguished from Monomatapa by having the male opercula nearly parallel-sided, rounded and meeting or almost meeting rather than tending linear and tear-drop shaped and clearly separated, the width of the male abdomen being equal to that of the thorax rather than notably wider, and the apices of the uncal lobes simply pointed rather than double-pointed.

Differentiation from *Abroma* is relatively subtle; the conjunctival claws of *Abroma guerinii*, the type species of Abroma, are apically bifurcate rather than simple and the pygofer basal lobes are more developed.

**Remarks.** My limited study of *Abroma* supports Boulard's (1979, 1990) suggestion that *Abricta* and *Abroma* may be synonymous. However, a full appraisal of all *Abroma* species should be undertaken, and this falls beyond the limits of this study; consequently the synonymy of *Abricta* and *Abroma* will not be pursued here.

**Distribution**. Restricted to the islands of Mauritius and Reunion.

**Behaviour**. Unconfirmed reports (O. Griffiths, pers. comm.) say adult males perch head down.

#### Key to species of Abricta s.str.

1 A large species, width of head including eyes exceeding 10 mm			
	(Mauritius) ferruginosa St	tål	
	A medium to small species, width of head including eyes never		
	greater than 9 mm (Mauritius and Reunion Islands)	ıs)	

# Abricta brunnea (Fabricius, 1798)

Figs. 19, 37, 38, 40a,b

Tettigonia brunnea Fabricius, 1798: 517; Fabricius, 1803: 18, 43; Donovan, 1820: [41: Zimsen, 1964: 291.

Cicada brunnea.—Germar, 1830: 42; Burmeister, 1835: 182; Walker, 1850: 230; Dohrn, 1859: 75.

Tibicen brunnea.-Stål, 1861: 618.

Tibicen (Abricta) brunneus.—Stål, 1866: 26; Atkinson, 1886: 187; Distant, 1892a: 131; Kirby, 1893: 178; Melichar, 1904: 26.

Tibicen brunneus.—Stål, 1870: 8; Atkinson, 1885: 157; Atkinson, 1886: 188.

Abricta brunnea.—Karsch, 1890: 121; Karsch, 1891: 348; Distant, 1905a: 27; Distant, 1906: 130; Orian, 1954: 235; Orian, 1956: 651; Mamet, 1957: 73; Metcalf, 1963: 205–206; Boulard, 1979: 28–30, 31, 33, 35, 44, 45; Duffels & van der Laan, 1985: 234; Boulard, 1990: 209, 210.

**Types**. Two presumed syntype males (UZMC, ex University of Kiel collection), one labelled "brunnea" (apparently in Fabricius' hand) and "TYPE" (red, machine-printed label); the other specimen is unlabelled.

Lectotype designation. Fabricius (1798) described this species without stating the number of specimens examined, recording only the locality and collector as "in Isle de France Dom. Daldorff". However, five years later Fabricius (1803) listed two specimens as being in his collection at the University of Kiel. Zimsen (1964) listed both specimens as now being in UZMC (see above). It is reasonable to assume that Fabricius may have based his description on both these specimens. To clarify the identity of the species and follow the apparent intentions of Fabricius the male labelled "Type" is here designated lectotype and the other paralectotype.

Material examined. Type as above and the following. MAURITIUS: 19, 1837, Desjardins; 13, 1838, Desjardins; 13, 1901, Ch. Alluaud; 13, 60, Ray. Mamet, Coll. R. Mamet; 13, Reduit, R. Mamet, Coll. R. Mamet (all labelled Ile Maurice and det. Michel Boulard, 1978) (MNHP).

#### **Description**

Male (Figs. 19, 37, 38, 40a). Head. Black or nearly black but sometimes partly dark ferruginous, usually with a small ochraceous spot on dorsal midline against posterior margin. Postclypeus glossy black with a narrow muddy pale yellow margin extending sometimes partially to dorsal region. Anteclypeus glossy black. Rostrum black with basal region brown or dull yellow; reaching bases of hind coxae. Antennae brown to nearly black. Bearing some indistinct silver pubescence, more obvious below. Thorax. Pronotum ochraceous with ferruginous markings; a broad ferruginous fascia on midline, spreading laterally at its posterior end against pronotal collar and to a slightly smaller degree at its anterior end, the shape of this fascia somewhat variable between individuals; broken ferruginous patches following

pronotal grooves and transversely between first and second grooves; also a narrow ferruginous border around ochraceous area, broadening laterally; pronotal collar ferruginous. Mesonotum dark ferruginous with much of dorsal region often tending brown with a dorsal pair of dark ferruginous obconical markings based on anterior margin, and sometimes a much larger lateral pair of similar obconical markings; cruciform elevation usually brown, sometimes dark ferruginous. Thorax below brown rather than dark ferruginous and usually bearing obvious silver pubescence. Wings. Hyaline, usually with a faint brownish tint. Fore wing basal cell tinted golden brown; venation brown with much of costal margin ferruginous; basal membrane orange basally becoming blackish, sometimes almost entirely black. Hind wing plaga muddy white to brown, very broad along 3A almost to its distal end and along inner margin, these two almost meeting, also very narrow plaga along 2A to or near to its distal end; venation brown. Legs. Brown, variable in tone both on individuals and between individuals. Opercula. Light yellowish brown; extending to or just beyond margins of tympanal cavities, never quite meeting; usually covered to a large degree by fine silver pubescence. Abdomen. Tergites ferruginous brown, usually dark. Sternites similar in colour to tergites but sternites III–VI usually with a narrow, orange-brown distal margin. Abdomen above and below often with silver pubescence. Tymbals (Fig. 19). Bearing 14 long ribs, otherwise as for generic description. Genitalia (Figs. 37, 38). Pygofer ferruginous; upper pygofer lobes in lateral and ventral views small and rounded; secondary upper pygofer lobes in lateral view sharply pointed and lying just below upper lobes, in ventral view conical with apex rounded; basal lobes in lateral view barely visible, in ventral view broad, angular with slightly rounded apex. Uncal lobes terminating in thick-set, down-turned lobes, in ventral view tapering to a blunt point. Conjunctival claws directed ventrally, very small, claw-like, simple.

**Female** (Fig. 40b). Colour and markings similar to male. Abdominal segment 9 ferruginous brown. Ovipositor sheath dark ferruginous, extending almost 1 mm beyond distal end of dorsal beak.

**Measurements.**  $n = 3 \ \frac{3}{6}, 1 \ \frac{9}{6}$  (includes all available specimens). *Length of body*: male 19.9–21.5 (21.0); female 24.0. *Length of fore wing*: male 26.0–28.0 (27.1); female 29.8. *Width of head*: male 7.1–7.5 (7.3); female 8.2. *Width of pronotum*: male 7.0–7.6 (7.4); female 8.2.

**Distribution**. Mauritius and Reunion Islands. Records from Italian Somaliland (Melichar, 1904) and Bengal (Stål, 1866; Atkinson, 1885) are probably erroneous as they are based on single records from localities far removed from records of positive origin.

# Abricta ferruginosa (Stål, 1866)

Figs. 41a,b, 42, 43

Tibicen (Abricta) ferruginosus Stål, 1866, 27. Abricta ferruginosa.—Karsch, 1890: 121; Karsch, 1891: 348; Distant, 1906: 130; Orian, 1954: 235; Orian, 1956: 651; Mamet, 1957: 73; Metcalf, 1963: 208; Orian, 1964: 1–3; Dugdale, 1972: 858; Duffels & van der Laan, 1985: 234–235; Boulard, 1990: 209.

Type. Location unknown.

Material examined. MAURITIUS—1♂, G. Autelme, Pres. by Imp. Bur. Ent. Brit. Mus. 1926-403 (no other data apart from Mauritius); 1♂, Ile Maurice, Desjardins 2901-40, 338, Distant Coll. 1911-383 (BMNH). 1♂, Reduit, 2.x.[19]53, P. Le Merle, Coll. R. Mamet; 1♂, 87, Ray. Mamet; 1♂, 43, Ray. Mamet, Coll. R. Mamet; 1♂, Curepipe, [?]1903, Coll. R. Mamet; 1♂, Desjardins 2771-36 (all labelled Mauritius or Ile Maurice and det. Michel Boulard, 1978) (MNHP).

# **Description**

Male (Figs. 41a, 42, 43). Head. Black with a muddy yellow or brown spot on dorsal midline against posterior margin and sometimes this coloration expanded a little along posterior margin, also sometimes brown on outer margin of lorum. Postclypeus ferruginous brown to dominantly black, usually with black to varying degrees dorsally and as a broad band along ventral midline; a narrow muddy yellow margin laterally of variable length. Anteclypeus black, sometimes tending brown, especially at distal end. Rostrum black but usually with basal region partly brown; reaching to bases of hind coxae. Antennae brown to nearly black. Head usually with some silver pubescence, mainly confined to underside. *Thorax*. Pronotum ochraceous with black or nearly black markings to varying degree; nearly always with a broad, black fascia on midline spreading laterally at its posterior end against pronotal collar and to a smaller degree at its anterior end which falls just short of pronotal anterior margin; often this fascia internally brown along midline on anterior half; usually with a cluster of black mottling between first and second pronotal grooves and overlaying second groove; black also laterally; never black along anterior margin between eyes; pronotal collar ochraceous to dark ferruginous or a mixture of both, but usually becoming black laterally at or beyond lateral angles. Mesonotum dark ferruginous with a pair of indistinct middorsal obconical dark ferruginous markings based on anterior margin, defined only by a thin ill-defined pale margin; cruciform elevation also dark ferruginous. Ventrally brown rather than dark ferruginous and usually with obvious silver pubescence. Wings. Hyaline but usually with faint brownish tint. Fore wing basal cell tinted golden brown; venation brown with much of costal margin ferruginous; basal membrane brown to blackish. Hind wing plaga muddy white to brown, very broad along vein 3A almost to its distal end and along inner margin with intermediate area bearing dark brown suffusion, also very narrow plaga along vein 2A to its distal end; venation brown. Legs. Ferruginous brown; distal ends of femora usually indistinctly marked yellow, fore femora also usually indistinctly yellow along line of femoral spines. Opercula. Mid to dark brown; rounded, extending to or just beyond margins of tympanal cavities, meeting or very nearly meeting; usually covered to a large degree by fine silver pubescence. Abdomen. Tergites dark ferruginous but tergite 2 sometimes indistinctly pale along its anterior margin. Sternites similar in colour to tergites but sternites III-VI usually with a narrow, orange-brown distal margin. Abdomen above and below often with silver pubescence. Tymbals. Bearing 11– 12 long ribs, otherwise as for generic description. Genitalia (Figs. 42, 43). Pygofer ferruginous; upper pygofer lobes in lateral view small and rounded, in ventral view broad and rounded; secondary upper pygofer lobes in lateral view pointed and lying just below upper lobes, in ventral view terminating in a tooth-like projection; basal lobes in lateral view barely visible, in ventral view broad, tending angular with rounded apical region. Uncal lobes each terminating in thick-set, down-turned lobe with apex in ventral view bearing a short blunt projection on its outer margin. Conjunctival claws directed ventrally, very small, clawlike, simple.

**Female** (Fig. 41b). Colour and markings similar to male except that cruciform elevation is a little paler than remainder of mesothorax on the single available specimen. Abdominal segment 9 ferruginous tending partly brown laterally. Ovipositor sheath dark ferruginous, extending almost 1 mm beyond distal end of dorsal beak.

**Measurements.** n =  $6 \ \delta \ \delta$ ,  $1 \$  (includes all available specimens). *Length of body*: male 28.5–31.4 (29.9); female 32.1. *Length of fore wing*: male 38.6–46.8 (43.0); female 45.9. *Width of head*: male 10.2–11.3 (10.9); female 11.1. *Width of pronotum*: male 11.0–12.9 (12.0); female 12.4.

**Remarks**. This species is markedly larger than *Abricta brunnea*; in fact, within the *Abricta* complex of genera it is the largest.

Orian (1964) studied the male genitalia of this species, especially the aedeagus. However, I had difficulty in relating some details of his figures to reality, particularly the attachment of the conjunctival claws to the distal end of the theca and the uncal lobes. His description of the cornu also differed from my dissection in relation to the spines that appeared to lie in the opposite direction. Three males of this species in BMNH have had their genitalia removed and these may well have been those examined by Orian. However, the genitalia preparations are apparently lost, it is not possible to assess Orian's interpretations fully.

**Distribution**. Known only from Mauritius where, at times, it is common (Boulard, 1979).

**Habitat**. Adults inhabit upland rainforest (known locally as maccabe forest), preferring tree trunks below the canopy (O. Griffiths, pers. comm.).

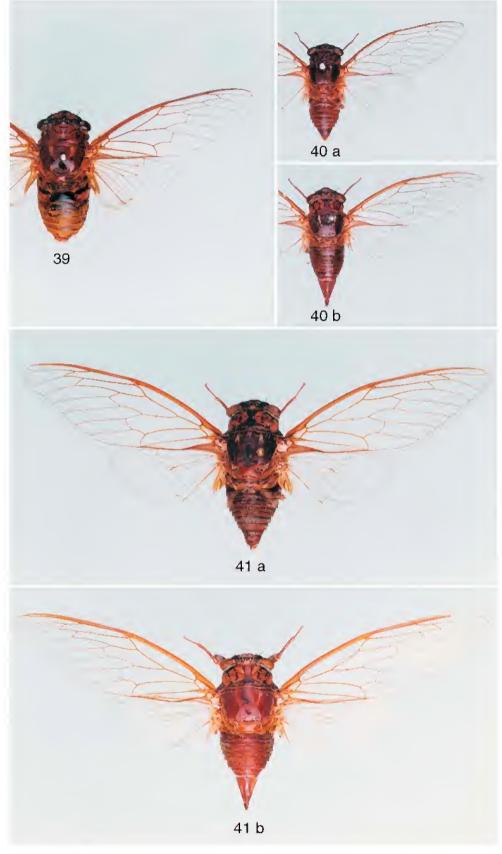
# Genus Chrysolasia n.gen.

Type species: Tibicen guatemalenus Distant, 1883.

Included species: guatemalena (Distant).

**Etymology**. From the Greek *chrysos* meaning gold and *lasios* meaning hairy, woolly or shaggy and pertaining to the golden body hairs of the type species, *guatemalena*.

**Diagnosis.** Postclypeus only slightly produced. Rostrum reaching to about bases of hind coxae. Width of head including eyes greater than anterior pronotum and nearly equal to mesonotum; width of male abdomen greater than width of thorax. Pronotal collar narrow with lateral angles



Figs. 39–41. Trismarcha and Abricta spp. (39) Trismarcha umbrosa Karsch, male. (40) Abricta brunnea (Fabricius); a, male; b, female. (41) A. ferruginosa (Stål); a, male; b, female. Approx.  $1.3 \times$  natural size.

ampliate and rounded; rudimentary and essentially confluent with adjoining sclerites anterior of lateral angles. Wings hyaline but with a very weak translucent brown tint. Fore wing without infuscations; costal margin moderately ampliate to node, the maximum dilation slightly less than width of costal vein, nodal line intersection near midpoint of ulnar cell; basal cell with translucent pigmentation. Hind wing plaga broad along much of vein 3A plus inner margin of anal lobe, narrower along vein 2A; light infuscation on wing margin at distal end of 2A, mostly on margin of anal lobe. Tymbals with 8 long ribs evenly spaced but slightly converging dorsally; basal plate small (Fig. 21). Male opercula linear, tending tear-drop in shape, weakly angled inwards before midpoint; nearly flat; just meeting and extending laterally and distally a little beyond tympanal cavities. Body bearing golden pubescence, possibly extensive on newly emerged individuals.

Male genitalia (Figs. 35, 36) with pygofer dorsal beak large, long and pointed; upper pygofer lobes moderately developed, pointed, undivided; pygofer basal lobes divided, outer lobe broad and rounded, inner secondary lobe pointed in lateral view. Uncal lobes broad, disc-like, tending towards meeting but never doing so, each terminating in a thick-set, down-turned blunt projection; uncal lateral processes absent. Aedeagus in lateral view gently curved for most of its length, basal plate a fused pair of nearly circular discs; conjunctival claws directed laterally and slightly ventrally, claw-like with no associated sclerotization, long and slender, strongly recurved, length about equal to diameter of theca, apex simple and pointed; flabellum and palearis absent.

#### Female. Unknown.

**Distinguishing features.** Within the Abricta complex of genera, golden abdominal pubescence is found only in this monotypic genus, the species of all other genera having silver pubescence. It is also the only genus in which the apex of the upper pygofer lobes are straight and pointed, in which the nodal line intersection lies near midpoint of ulnar cell and only 8 tymbal ridges. Although the broad, disclike uncal lobes are found also in Abricta, Abroma and Monomatapa, Chrysolasia differs in its more developed conjunctival claws which are directed laterally rather than ventrally, strongly recurved and are nearly equal in length to width of theca rather than much shorter. Other features of Chrysolasia are the broad male abdomen that is clearly wider than the thorax, and the linear and somewhat teardrop shaped male opercula, both attributes shared only with Monomatapa. Chrysolasia differs from Monomatapa (in addition to the autapomorphies of *Chrysolasia* mentioned above) by having male upper pygofer lobes of moderate proportions compared to exceedingly small upper lobes in Monomatapa, well-developed secondary basal lobes which are absent in *Monomatapa*, and uncal lobes that are simply pointed whereas those of *Monomatapa* are double pointed (compare Figs. 35, 36 with 33, 34).

**Distribution**. Recorded from Guatemala but this locality requires confirmation (see discussion of distribution under *C. quatemalena*).

# Chrysolasia guatemalena (Distant, 1883), n.comb.

Figs. 21, 35, 36, 51

Tibicen guatemalenus Distant, 1883: 18, pl. 2. Tibicen guatemalanus [sic].—Distant, 1892b: 64. Abricta guatemalena.—Distant, 1906: 131.

**Type**. Syntype &, bearing five labels: (a) "Purula,/Vera Paz./ Champion." machine printed; (b) "Tibicen/guatemalenus/ Dist" in india ink probably in Distant's handwriting; (c) "B.C.A.Homopt.I./Tibicen/guatemalenus,/Dist." machine printed; (d) "Type", machine printed on circular white label with red border; (e) "SYN-/TYPE" machine printed on circular white label with blue border (examined). (BMNH).

The original description by Distant (1883) suggests that there was probably only a single specimen available to him but this was not explicitly stated. While it is possible that he only had the one specimen listed above, following Recommendation 73F of the Code the specimen is retained as a syntype.

Type locality. Purula, Vera Paz, [? = Purulhá, Guatemala]. Distant (1883) described this species in a review of South American cicadas, recording it as coming from Guatemala. In fact he was so certain that it came from Guatemala he named it *guatemalenus*. However, the apparent absence of other related species within the Neotropics (and a lack of subsequent records) casts suspicion upon the accuracy of the type's label data and/or its interpretation. Purulia is a town in northern India and this locality would fit much better in the distribution patterns of the *Abricta* complex of genera. Nevertheless, a South American origin for this species cannot be dismissed and therefore Purula, Guatemala, is here accepted as the type's origin.

**Material examined**. Type male detailed above (the only known specimen).

#### Description

Male (Figs. 21, 35, 36, 51). Head. Nearly black with supraantennal plates tending muddy yellow, a small muddy yellow spot on dorsal midline against posterior margin. Postclypeus muddy pale yellow. Anteclypeus black tending brown. Rostrum muddy yellow tending black towards apex, passing just beyond bases of hind coxae. Head with silver pubescence, mainly confined to lora. Thorax. Pronotum dark ferruginous; a broad black fascia on dorsal midline spreading laterally at its posterior end against pronotal collar, this fascia internally brown along midline; pronotal collar dark ferruginous. Mesonotum dark ferruginous brown with a large black mark anterior of cruciform elevation and a black fascia laterally against wing groove; cruciform elevation dark ferruginous. Thorax below muddy yellow with silver pubescence. Wings. Hyaline with a faint brownish tint. Fore wing basal cell distinctly brown; venation and costa brown; basal membrane orange brown. Hind wing plaga brown, broad along vein 3A to near its distal end and along inner margin, very narrow plaga along vein 2A to its distal end; venation brown. Legs. Light yellowish brown without obvious markings; bearing very fine silver pubescence. Opercula. Pale yellow-brown; somewhat tear-drop in shape, extending just beyond tympanal cavities to conceal tympana completely, laterally confluent with abdominal margin, very nearly meeting; bearing fine silver pubescence. Abdomen. Tergites black except for brown lateral region to tergite 2. Sternites brown with posterior margins pale, sternites VII and VIII mostly pale. Abdomen above and below with golden pubescence. *Tymbals* (Fig. 21). As for generic description. *Genitalia* (Figs. 35, 36). Pygofer nearly black; upper pygofer lobe in lateral view small, broad at base and tapering to a blunt, off-centre point, in ventral view tilted inwards and tapering to a blunt point; basal lobes in lateral view small and tapering to a rounded apex and nearly equal in length to upper lobes, secondary basal lobes in lateral view small and sharply pointed. Uncal lobes terminating in a thick-set downturned lobe with apex bluntly pointed, in ventral vein gently incurved. Conjunctival claws claw-like, long, strongly recurved in dorsal view.

Female. Unknown.

**Measurements**.  $n = 1 \delta$  (the only available specimen). *Length of body*: 21.7. *Length of fore wing*: 27.3. *Width of head*: 7.7. *Width of pronotum*: 12.9.

**Distribution**. Known only from the male type, reputedly from Guatemala.

#### Genus Aleeta n.gen.

Type species. Cicada curvicosta Germar, 1834.

Included species. curvicosta (Germar).

**Etymology**. Derived from the Greek *aleton* meaning flour or meal and pertaining to the flour-like "dusting" partly covering the body of *A. curvicosta*, resulting from the fine silver body pubescence. This pubescence is easily abraded and is often substantially lacking on older adults.

Diagnosis. Postclypeus slightly produced. Rostrum reaching or just passing bases of hind coxae. Width of head including eyes equal to, or slightly wider than, anterior pronotum and equal to, or narrower than, mesonotum; width of abdomen as wide as thorax. Pronotal collar narrow with lateral angles ampliate and rounded; rudimentary and essentially confluent with adjoining sclerites anterior of lateral angles. Wings hyaline. Fore wing with infuscation at bases of apical cells 2 and 3; costal margin ampliate to node, the maximum dilation greater than width of costal vein; basal cell usually with translucent pigmentation. Hind wing with plaga along much of vein 3A plus inner margin of anal lobe and along length of vein 2A; plaga bordered by black infuscation that is partly expanded along wing margin at distal end of 2A. Tymbals (Fig. 20) with 11-13 long ribs (usually 12) evenly spaced but slightly converging dorsally; basal plate small. Male opercula tending tear-drop in shape, weakly angled inwards before midpoint; nearly flat; not quite meeting; extending laterally beyond lateral margins of abdomen and distally a little beyond tympanal cavities. Newly emerged individuals bear fine silver pubescence over much of body and along basal fore wing veins.

Male genitalia (Figs. 46, 47) with apical spine of pygofer large, long and pointed; upper pygofer lobes much shorter than apical spine, tending bilobed; pygofer basal lobes divided into primary outer and secondary inner lobes, the outer lobe in lateral view substantially webbed to inner lobe. Uncal lobes widely separated, beak-like, downturned; no lateral process at base of uncus. Aedeagus in lateral view straight or gently curved for most of its length, basal plate

a fused pair of nearly circular discs; conjunctival claws directed ventrally, claw-like with no associated sclero-tization, flattened, broad in lateral view, narrow in ventral view, apex simple and pointed; a small sublateral rounded flange either side of theca near distal end; palearis absent.

Female abdominal segment 9 long, clearly more than half as long as abdominal remainder, nearly conical; ovipositor (Fig. 8) long with strong dorsal downward slope in lateral view; ovipositor sheath terminating about level with, or slightly extending beyond, apex of dorsal beak.

**Distinguishing features**. Male genitalia show features unique within the *Abricta* complex of genera: the beak-like uncal lobes and the partially bifurcate upper pygofer lobes do not occur elsewhere in the *Abricta* complex, while the pair of sublateral flanges near the distal end of the theca and the laterally flattened conjunctival claws are unknown in any other Cicadoidea. The broad male opercula, which extend clearly beyond the lateral margins of the abdomen, are also unique within the *Abricta* complex of genera. The strongly ampliate fore wing costa is shared with *Tryella* but is otherwise only found in a few distantly related genera.

Remarks. The distinctive nature of this monotypic genus is also reflected in its genetic makeup. Allozyme electrophoresis revealed a high number of fixed differences between *A. curvicosta* and some allied species examined, reflecting the high genetic dissimilarity and long genetic distance between *A. curvicosta* and *Tryella* species (Serkowski & Moulds, unpub. data). Further, phylogenetic analyses of both electrophoretic and morphological data confirm the evolutionary distinctiveness of *A. curvicosta* from its sister group *Tryella* (Serkowski & Moulds, unpub. data, and Figs. 15–17). See also discussion under *Rationale for new taxa* (pp. 254–255).

**Distribution**. The single species included in this genus occurs in eastern Australia from northern Queensland to southern New South Wales.

#### Aleeta curvicosta (Germar, 1834), n.comb.

Figs. 8, 20, 46, 47, 50a-f, 60

Cicada curvicosta Germar, 1834: 66–67; Walker, 1850: 114; Dohrn, 1859: 73; Stål, 1859: 270; Bennett, 1860: 271; Ewart, 1990: 3. Cicada tephrogaster Boisduval, 1835: 610–611, pl. 10.

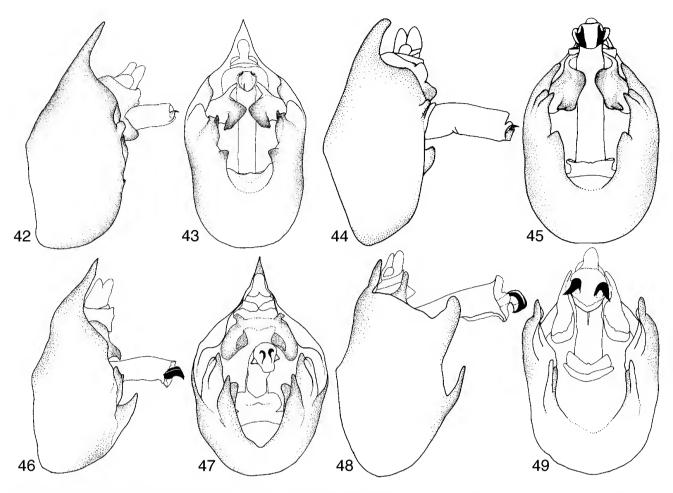
Tibicen curvicostus.-Stål, 1861: 618.

Tibicen (Abricta) tephrogaster.-Stål, 1866: 26.

Tibicina curvicosta.-Froggatt, 1903: 418.

Tibicen curvicosta.-Goding & Froggatt, 1904: 565, 599-600.

Abricta curvicosta.—Distant, 1906: 130; Froggatt, 1907: 351; Kirkaldy, 1907b: 308; Ashton, 1914: 349; Froggatt, 1914: 341; Distant, 1920: 457; Singh-Pruthi, 1925: 194, pl. 20; Chisholm, 1932: 131; Kato, 1932: 181, pl. 28; Froggatt, 1933: 93; Finlayson, 1934: 232; McKeown, 1942: 98; McKeown, 1944: 234, 237; Anonymous, 1948: 1; Musgrave, 1953: 15; Tillyard, 1926: 161; Kato, 1956: 61, pl. 14; Burns, 1957: 635, 636; McKeown, 1958: 380; Metcalf, 1963: 206–207; Orian, 1964: 1; Wilson, 1970: 22; Woodward et al., 1970: 413; Young, 1972a: 343, 352–355; Young, 1972b: 238, 241, 242, pls. 1, 3; Young, 1973: 377, 378; Michelsen & Nocke, 1974: 257; McAlpine, 1977: 25; Noyce, 1980: 9; Hockings, 1980:99; Moulds, 1983: 434; Young & Josephson, 1983b: 198, 204, 206; Duffels & van der Laan, 1985: 234; Mac Nally & Doolan, 1986a: 281, 284–291; Mac



Figs. 42–49. Male genitalia of *Abricta, Abroma, Aleeta* and *Tryella* species showing pygofer with uncus and aedeagus in right lateral view (left) and ventral view (right): (42–43) *Abricta ferruginosa*, Mauritius; (44–45) *Abroma guerinii*, Madagascar; (46–47) *Aleeta curvicosta*, genitalia prep. AB32; and (48–49) *Tryella noctua*, genitalia prep. AB21.

Nally & Doolan, 1986b: 35, 37–40, 42–43, 46; Clyne, 1990: 133; Moulds, 1990: 119–120, pl. 15; Moulds & Carver, 1991: 467; Boulard, 1991: 118; Ewart, 1995: 82; Moss, 1997: 10; Ewart, 2001a: 502–505, 507, 508; Ewart, 2001b: 69–75, 81–83.

#### **Types**

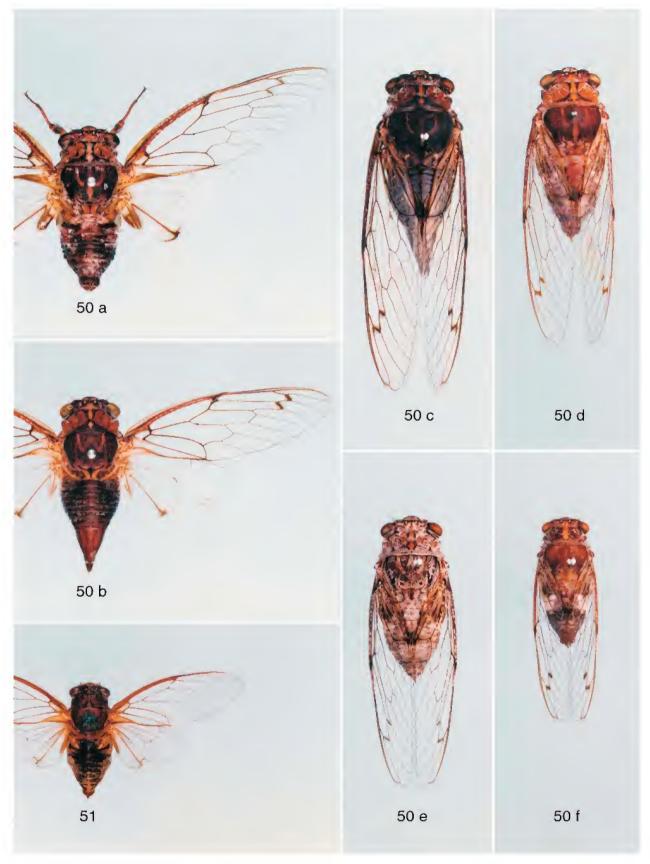
(a) Cicada curvicosta Germar. Lectotype  $\delta$  here designated and paralectotype  $\delta$  (in OUM). Lectotype  $\delta$  bearing three labels: (a) "Hem. Type No. 790 1/2"; (b) "NH" [= New Holland] white label handwritten in ink; (c) "curvicosta Germ" blue label handwritten in pencil. Paralectotype  $\delta$  bearing two labels (a) "Hem. Type No. 790 2/2"; (b) "NH" white label handwritten in ink.

Lectotype designation. Germar did not designate a type for curvicosta or list the specimens he examined. Ewart (1990) confirmed the existence of two specimens (both male) in the Hope Entomological Collections, Oxford, that could be regarded as syntypes. To ensure the identity of this species as previously known and to maintain the long established synonymy of curvicosta and tephrogaster the specimen (Hem. Type No. 790 1/2) is here designated lectotype. The remaining specimen (Hem. Type No. 790 2/2) is designated paralectotype.

Type locality. The type locality is known no better than Australia. Germar's types are labelled only as coming from New Holland while his description of the species simply gives the locality as "Habitat in Australasia".

(b) Cicada tephrogaster Boisduval. Lectotype & here designated and paralectotype & (in MNHP) (examined). Lectotype & bearing three labels: (a) "Portjacks./Durville" handwritten in india ink; (b) "Cicadal tephrogaster Bdv" in handwriting of Boisduval; (c) "Voyage de/l' Austrolabe/ Holotype & /Cicada/tephrogaster/Boisduval/Michel Boulard det. 1990" partly handwritten, partly machine printed. Paralectotype & bearing three labels: (a) "tephrogaster/Port Jackson/M. d'Urville" handwritten in india ink; (b) "Cicadal tephrogaster Boisd." in handwriting of Boisduval; (c) "Voyage de/l' Austrolabe/Paratype & /Cicada/tephrogaster/Boisduval/Michel Boulard det 1990" partly handwritten, partly machine printed.

Lectotype designation. Boisduval did not designate a type for tephrogaster or state the number of specimens he examined. Boulard (1991) confirmed the existence of two specimens (both male) in MNHP that should be regarded as syntypes. To ensure the synonymy of tephrogaster with curvicosta the specimen labelled holotype is here chosen as lectotype and the remaining specimen as paralectotype.



Figs. 50–51. *Aleeta* and *Chrysolasia* spp. (50) A. curvicosta (Germar); a,d,e,f, males; b,c, females; (51) C. guatemalena (Distant), male. Approx.  $1.4 \times$  natural size.

**Material examined**. Types and the following: QUEENSLAND—1 &, Cairns, 6-20.i.1962, Carne & Britton;  $4 \stackrel{?}{\circ} \stackrel{?}{\circ}$ ,  $5 \stackrel{?}{\circ} \stackrel{?}{\circ}$ , Bundaberg, 18.ix.1972, on trunk of Casuarina, H. Frauca; 1♀, Bin Bin via Didcot, 14.ix.1975, H. Frauca; 13, Brisbane, 2.i.[19]11, W.W. Froggatt Collection; all in **ANIC**. 1♂, Ravenshoe, 11.i.1962, E.B. Britton; 1♀, Peak Downs (no date or collector); all in **BMNH**. 1♀, Mt Molloy, 20.xii.1987, T.A. Moulds; 2♂♂, 6♀♀, Rifle Creek, Mt Molloy, 9.i.1992, L.R. Ring;  $3 \delta \delta$ , 4 9 9, Julatten, 1.iii.1979, 30.i.1980, 15.ii.1981, 4.i.1983, 19.xii.1985, 15.xii.1987, A. Walford-Huggins; 1♂, 1♀, Julatten, 27.i.1986, H. & J. Beste; 633, 1099, Julatten, 1.i.1977, 24.i.1981, 29.i.1982, 4.i.1984, 16.i.1988, MBM; 1♂, 1♀ (male genitalic preparation no. AB34), Julatten, 4.i.1980, A. Hiller; 299, Black Mtn Rd, 23 km from Kuranda, 27.i.1977, AMW-H; 13, 20 km N of Kuranda, 4.i.1978, A. Hiller; 1♀, Black Mtn Rd, Kuranda, 28.i.1979, R. Storey, I. Titmarsh; 5233, 3599, Kuranda, 25.xi.1987, 3.i.1988, 4.i.1988, 7.i.1988, and 10.i.1988, J. Hasenpusch; 9♂♂, 1♀ (1 male genitalic preparation no. AB38), Kuranda, 16.i.1960, M.S. Moulds; 1033, 1599, Kuranda, 29.xii.1976, 5.i.1977, 14.i.1977, 16.i.1977, 15.i.1988, MBM; 1&, Kuranda, 31 xii.1988, H. & A. Howden; 1&, Kuranda, 5-15.i.1976, J. McLoughlin; 1 \, Kuranda, 1-10.i.1987, C. Rojewski; 1♂, Kuranda, 4 i.1974, AMW-H; 4♂♂, 2♀♀, Kuranda, 29.i.1980, 30.xii.1982, 13,22,23.i.1983, G. Wood; 1♀, Myola, 10.i.1976, J. McLoughlin; 2♂♂, Myola, 6.i.1974, AMW-H; 1♀, Oak Forest, 8.iii.1973, A.P. & M. Walford-Huggins; 13, 12, Clohesy River S.F. SW of Kuranda, 18.i.1984, MBM; 1&, Mareeba Road, Clohesy R., 17.i.1974, AMW-H; 5♂♂, 1♀, Atherton, 18.i.1980, A. Irvine; 2♂♂, 2  $\mathfrak{P}$ , Atherton, 14,27.xi.1989, D.A. Lane; 2  $\mathfrak{F}$   $\mathfrak{F}$ , 2 km W of Atherton, 7.i.1990, D.A. Lane; 2 of of, (1 genitalic preparation no. AB41), Wondecla, nr Herberton, 4-8.i.1981, G. Wood; 19, 16 km W of Ravenshoe, 2.i.1975, M.S. Moulds; 19, Cairns, i.1960, M.S. Moulds; 18, Mulgrave R, 25 km S of Gordonvale, 30 m, 15,i,1980, A. Hiller; 1♀, Tully Gorge, 21.i.1990, J. Hasenpusch; 3♂♂, nr Garradunga, nr Innisfail, 6.xi.,5,31.xii.1987, J. Hasenpusch; 1♀, Storey Ck, Garradunga, 8.xii.1992, J. Hasenpusch; 1♂, 11♀♀, Kirrama Range, W of Kennedy, 17.i.1990, MBM; 2♂♂, Brandon, nr Ayr, 26.xii.1989, MBM; 1♂, 1♀, Ayr, 8.i.1967, M.S. Moulds;  $10 \circlearrowleft \circlearrowleft$ ,  $3 \circlearrowleft \circlearrowleft$  (1 male genitalic preparation no. AB30), Funnel Creek, 50 km SW of Sarina, 8.xii.1980, MBM; 8♂♂,5♀♀, Waverley Ck, Bruce Hwy, 10 km S of St Lawrence turnoff, 21.xii.1987, 23.i.1992, MBM;  $9 \circlearrowleft \circlearrowleft$ ,  $8 \circlearrowleft \circlearrowleft$ , Cathu State Forest, N of Eungella Nat. Pk, 600 m, 21.i.1990, 22.i.1992, MBM; 2♂♂, 3♀♀, same data but base of range 150 m; 1 d (genitalic preparation no. AB33), Eungella Nat. Park, W of Mackay, 10.i.1967, M.S. Moulds; 2♂♂, 1♀ (1 male genitalic preparation no. AB42), Gargett, W of Mackay, 14.i.1979, L.R. Ring; 13, 48 km S of Glenden Mine, 17.i.1987, MBM; 13, 19, Mackay, i.1985 and i-ii.1985, E.W.J. Adams; 19, Seaforth via Mackay, 1.i.1988, B. van Moolanbroek; 1♂, Rockhampton, 20.xii.1976, MBM; 1♂, Kawana, Rockhampton, 20.i.1984, R. Eastwood; 1♀, Yeppoon, 16.i.1992, A. Walford-Huggins; 2♂♂, Isaac R. x-ing N of Dingo/Mt Flora road, 27.i.1986, MBM;  $5 \delta \delta$ ,  $7 \circ \circ$ , McKenzie River x-ing 75 km NNE of Dingo, 17.i.1987, MBM; 5♂♂, Dawson R., 4 km SW of Mourangee Hsd, nr Edungalba, i.1985, E.E. Adams; 233, Dawson River, 7 km SW of Mourangee Hsd, nr Edungalba, 12.xii.1987, E.E. Adams; 1♂, 6 km SW of Mourangee Hsd, nr Edungalba, 20.xii.1987, T.A. Moulds; 1♂, 50 km S of Duaringa, 29.i.1986, MBM; 3♂♂, Christmas Creek, 43 km S of Rolleston, 20.xii.1983, MBM; 14♂♂, 8♀♀ (1 male genitalic preparation no. AB67), 85 km S of Rolleston, 20.xii.1983, MBM; 10, 60 km N of Biloela, 22.i.1982, MBM;  $11 \stackrel{?}{\circ} \stackrel{?}{\circ}$ ,  $15 \stackrel{?}{\circ} \stackrel{?}{\circ}$ , (1 male genitalic preparation no. AB66), Theodore, 23,24.xii.1989, R. Eastwood; 3♂♂, 11 km SSE of Wandoan, 22,xii,1989, MBM;  $4 \circ \circ$ , base, Mount Scoria, 6 km S of Thangool, 24°32'S 150°36'E, 10.ii.1991, GAD, C. Burwell; 5♂♂, 1♀, (1 male genitalic preparation no. AB36), Upper Granite Ck, S of Miriam Vale, 7.xii.1980, MBM; 1&, 30 km NE of Lowmead, 31.xii.1974, G.B. Monteith; 19, Bundaberg, 5.x.1982, J. North; 19, Bundaberg, 10.xi.1985, F.G. Sattler; 1♀, Wallaville, 20.xii.1972, G. Cook; 1♀, Mt Goonaneman, via Childers, 6-7.ii.1981, G.B. Monteith; 19, Burnett River, 10 km N of Eidsvold, 20.i.1988, MBM; 1&, Torbanlea nr Pialba, 20.i.1979, J.V. Peters; 1♂, Maryborough, 1.xi.1988, K.L. Dunn; 1♀, Maryborough, 23.xi.1986, R. Eastwood; 1♀, Gympie, 30.xi.1988, R. Eastwood; 1♂, Doonan, Noosa Valley, 31.i.1988, R. Eastwood; 5♀♀, Ningi, 27.xii,6.i.1992, G.R. Cleminson; 1♂, 2♀♀, 14 km N of Nambour, 24.i.1992, MBM; 2♂♂, Mudjimba Beach, Sunshine Coast, 5.i.1988, R. Eastwood; 1♂, Maroochydore, 1.xii.1985, K. Tyrer; 4♂♂, 899, Maroochydore, 5.xii.1978, 7,8,10.xii.1985, 1.ii.1987, 23.xi.1987, 30.xii.1987, 5,9.i.1988, 10.xii.1990, 16.ii.1991, R. Eastwood; 1&, The Cod Hole, Maroochydore, 6.xi.1985, R. Eastwood;

1♂, 1♀, Buderim, 1.i.1978 and 10.xi.1980, R. Eastwood; 1♂, Maleny, 30.xii.1977, R. Eastwood; 1♀, 30 mi N of Brisbane, 12 i.1973, P. Zborowski; 1♂, Somerset Dam, 19.i,1992, R. Eastwood; 1♀, Mt Nebo, 500 m, NW of Brisbane, 7.i.1986, A. Hiller; 1♂ (genitalic preparation no. AB40), Brisbane, 16.i.1973, M.S. Moulds; 13, Brisbane, 30.xi.1978, J. North; 1♀, Brisbane, 9.ii.1975, A. Walford-Huggins; 1♂, 1♀, Redcliffe, Brisbane, 9.xii.1983, R. Eastwood; 2♂♂, 1♀, Redland Bay, [Brisbane], 12,16.i.1992, R. Eastwood; 1&, Stafford, 26.ix.1985, S.R. Raine; 299, Jamboree Heights, Brisbane, 15.xii.1984, 22.xii.1990, G. Daniels; 1♀, Jamboree Heights, Brisbane, 13.xii.1979, A. Daniels; 1♂, Rainworth, Brisbane, 8.xii.1979, J. Conran; 13, Taringa, Brisbane, 6 x.1984, J.T. North; 5 & &, St Lucia, Brisbane, x.1983, 6.x.1984, 22.xii.1985 and 3.i.1986, R. de Keyzer; 1♂ (genitalic preparation no. AB32), St Lucia, Brisbane, 17.xii.1976, MBM; 13, 299, St Lucia, Brisbane, 27.i.1980, 24.ii.1980 and 13.xi.1980, C. Hagan; 2♂♂, St Lucia, Brisbane, 3.xii.1985, 5.ii.1990, G. Daniels; 13, Corinda, Brisbane, 7.i.1982, J. North; 19, Tarragindi, Brisbane, 20.vii.1984, J.T. North; 399, Doolandella, Brisbane, 11,12.i.1985, MBM; 136, Moogerah Dam, Aratula, 11.i.1993, R. Eastwood; 3♀♀, Isle of Capri, Gold Coast, 6.xii.1989, 9.xii.1989 and 13.i.1990, R. Eastwood; all in MSM. 1♂, Daintree R., [no date], K. Hateley; 1♂, Mt Molloy, 3.i.1954, G.B[rooks]; 6♂♂, 1♀, Kuranda, 14.i.1950, 28,29.i.1951, G.B[rooks]; 19, Cairns, [no date], Edmund Jarvis; 13, 19, Cairns Dist., 1945, S. Brock; 1♂, Mulgrave River, 26.xii.1926, A.N. Burns; 1♀, Mackay, 15.iii.30, A.N. Burns, Collection A.N. Burns [labelled allotype A. cadulua, an unpublished manuscript name]; 1♂, Westwood, 4.i.24, A.N. Burns, Collection A.N. Burns [labelled holotype of A. cadulua, an unpublished manuscript name]; 1♀, Noosa Heads, i.1962, [J.] Guyomar; 11♂♂, 499, Brisbane, 14.xii.1952, 12 & 21.ii, 27.xi, 10.xii.1954, 27.xii.1958, 27.xii.1959, 7.i.1961, J. Kerr; 2 & &, Mt Cootha, 12.iii.1955, J. Kerr; 2&&, Burleigh Heads, 3-4.i.1956, 26.i.1958, J. Kerr; 1&, Esk, 14.xii.1958, J.K[err]; all in MV. 19, Bundaberg, Baldwin's Swamp Survey 1992, Eric Zillman; 1&, Brisbane, 14.i.[19]13, H. Hacker; 19, Brisbane, 2.xii.[19]52, R.H. Magee; 19, Mus[eum] Brisbane, 31.i.[19]52, D.P. Vernon; 1&, Wilston, Brisbane, 5.i.[19]61, B. Poyser; 16, Inglewood (no other data); 366, 19, "Glen Witheren", Canungra Creek, 20-22.i.1987, G.B. Monteith; 19, Cunningham's Gap, New Year 1962 (no other data); all in **QM**. 1♀, Gordonvale, 13.i.[19]49, B. Hitchcock; 1♀, Tully, iii.1961, A. Flegler; 1♀, Townsville, 15.viii.[19]57, I. Sutherland; 1&, Greta Ck, 20 mi N of Proserpine, 1.i.1965, G. Monteith; 1♀, Springsure, 7.xi.1950, D.G. Tulloch; 1♀, Colosseum Ck, 10 mi S of Miriam Vale, 20.xii.1966, B. Cantrell; 1&, Biloela, 21.i.[19]47, F. Kleinschmidt; 1♀, 20 mi S of Biloela, 7.i.1972, B. Cantrell; 1♂, 2♀♀, 30 km NE of Lowmead, 31.xii.1974, G.B. Monteith; 13, Planted Ck, via Tansey, 12.xii.1976, G.B. & S.R. Monteith; 19, Gympie, 9.ii.[19]45, M. Sauer; 1&, Gympie, 20.xi.1965, B.A. Mooney; 13, M'ydore [= Maroochydore], 25.xii.[19]21, J.A. Beck; 13, Lawes, xii.[19]54, J. Thapa; 1♂, Gatton, 14.xii.[19]34; 1♀, Brisbane, 11.viii.[19]57, G. Diatloff; 13, Brisbane, 4.i.[19]43 (no other data); 1∂, Brisbane, 1.xi.[19]57, P. Ranby; 1♀, Tingalpa, [Brisbane], 21.i.[19]56, G.E.; 233, Brisbane, 28.i.,14.ii.1951, C. Deane; 13, Brisbane, 16.i.[19]50, R. Domrow; 19, St Lucia, [Brisbane], ii.1959, I. Rowlingson; 1♀, Brisbane, i.1961, R.G. Winks; 1♂, Redland Bay, [Brisbane], 19.xi.[19]62, G. Shaw; 1&, Warwick, 1.i.[19]55, R.W. Downes; all in UQIC. NEW SOUTH WALES—19, Dorrigo [no other data], Collaroy [Sydney], 2.i.1959, K.R. Norris; 19, Gerringong, i.1926, M. Fuller; all in ANIC. 16, Parramatta (no date or collector) BMNH. 13, Nabiac, 2.xii.1966, L.R. Greenup; 13, Terrigal, 2.i.1970, L.R.G[reenup];  $1\delta$ , East Gosford, 28–29.xi.1964, P.C. Hely; 1, Wiseman's Ferry, ii.1964, R. Craig; 16, Earlwood, Sydney, 29.i.1959, L.G[reenup]; 18, Cabramatta, [Sydney], 20.i.1963, M. Nikitin; all in LG. 1∂, Chinderah, Tweed River, 9.i.1985, MBM; 2∂∂, 1♀, Mt Warning, 300 m, 20.i.1988, R. Eastwood; 1 d, Kilgra, approx. 10 km N of Kyogle, 11.i.1976, W. Rixon; 1♂, Upper Eden Creek, nr Kyogle, 12.i.1967, M.S. Moulds; 1♂, Upper Eden Creek, nr Kyogle, 8.i.1985, MBM; 1&, Kyogle, 10.i.1975, M.S. Moulds; 1&, Lismore, 3 xii.1986, S. & B. Underwood; 19, Tregeagle, 10 km SW of Lismore, 20.i.1980, D. Yeates; 2♂♂, Konorogan [= Konorigan], 17.i.1965, G.R. Brown; 1♀, Wyrallah, 1.i.1967, G.R. Brown; 1♂, Pimlico, 12.i.1993, B. Thomas; 1∂, Black Swamp Tenterfield, 19.xii.1980, F.G. Sattler; 1∂, Coffs Harbour, 2.i.1971, M.S. Moulds; 2♂♂, Coffs Harbour, 10,20.i.1972, S. Devine; 13, 19, Coffs Harbour, 14,17.xii.1987, B.C. White; 13, Sawtell, 15.xii.1987, B.C. White; 19, Bellingen, xii.1987, K. Slater; 1♂, Urunga, 24.i.1971, M.S. Moulds; 2♀♀, Port Macquarie, 10.i.1972, M.S. Moulds;  $20 \stackrel{?}{\circ} \stackrel{?}{\circ}$ ,  $9 \stackrel{?}{\circ} \stackrel{?}{\circ}$  (1 male genitalic preparation no. AB39), Lansdowne, nr Taree, 27.xi.1980, MBM; 1♀, Lansdowne, 26.xi.1980, G. & T. Williams; 2♂♂, 2♀♀, 3 km N of Lansdowne, nr Taree, 7–

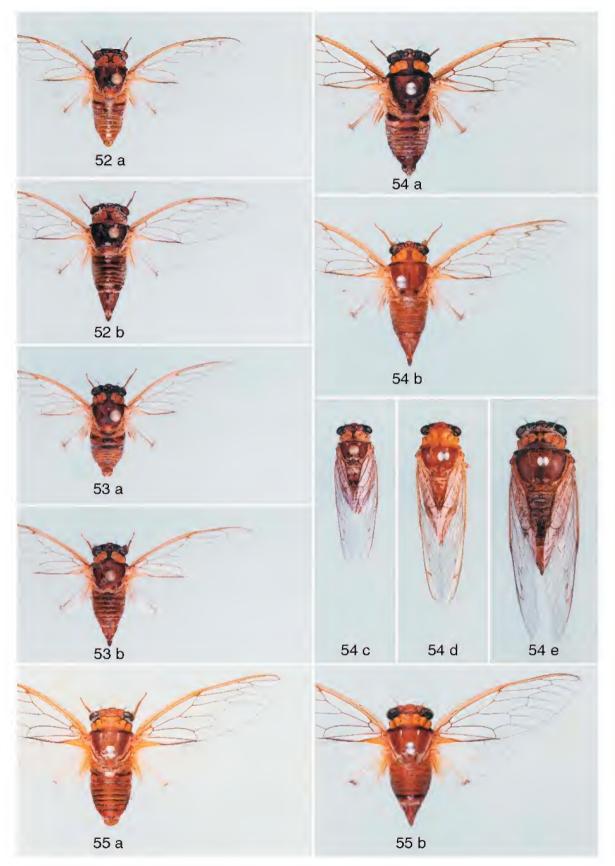
13.xii.1987, 30.xi-6.xii.1987 and 21-27.xii.1987, G. Williams; 1♂ (genitalic preparation no. AB35), Old Bar nr Taree, 8 i.1972, M.S. Moulds; 1♀, Dudley, Newcastle, 18.ii.1988, A. Atkins; 11♂♂, 8♀♀, Cardiff. Newcastle, 26.xi.1991, 1,2,6,20,30.xii.1991, 11,18,20,21,27.i.1991, F.G. Sattler; 1♂, 1♀, Charmhaven, 25.xi.1989, MBM; 1♂, Charmhaven, 23.xi.1990, A. Holmes; 1♀, Wheeny Ck, N of Kurmond, 22.ii.1992, MBM; 1&, Ourimbah S.F., 19.i.1988, B.C. White; 1 &, Avoca Beach, nr Gosford, 23.xi.1985, S. Hunter & A. Johnson; 13, 299, Avoca Beach, i.1979, 3.xii.1983, S. Hunter; 233, 19, Saratoga, nr Gosford, 9.xii.1985, Darley-Bently; 1♂, Barrenjoey, 10.i.1970, J.V. Peters; 1♀, Bayview, nr Church Point, 21.xii.1981, L.C. Haines;  $22 \stackrel{?}{\circ} \stackrel{?}{\circ}$  (1 male genitalic preparation, no. AB37),  $2 \stackrel{?}{\circ} \stackrel{?}{\circ}$ , Avalon Beach, Sydney, 20.xii.1958, 18.i.1962, 13.i.1963, 27.xii.1969, 28.xii.1969, 29.xii.1969, 1.i.1970, 2.i.1970 and 26.xii.1973, M.S. Moulds; 13, 19, Narrabeen, Sydney, 30.xii.1971, M.S. Moulds; 13, 499, Narrabeen, 30.i.1985, 12.xii.1985, i.1986 and ii.1990, G. Hangay; 5♂ ♂, Long Reef, 5.i.1972, J.V. Peters; 1♀, Forestville, Sydney, 18.xii.1987, T.I. Wallace; 1♀, Lane Cove, Sydney, 11.i.1988, S. & B. Underwood; 13, Lane Cove, 12.ii.1972, [no collector]; 13, Narremburn, Sydney, 3.xii.1979, C. Holmes; 2♂♂, 3♀♀, Greenwich, Sydney, 1.ii.1969, 20.xii.1969, 20.i.1970, 2.ii.1970 and 27.xii.1973, M.S. Moulds; 13, Greenwich, Sydney, 16.xii.1975, MBM; 233, 19, Greenwich, Sydney, 19.xii.1975 and 3.ii.1983, T.E. Moulds; 23 3, Greenwich, Sydney, 19.i.1974, C. Holmes; 3♂♂, 3♀♀ (1 male genitalic preparation no. AB31), Gymea, Sydney, 2.ii.1979, R. Eastwood; 1 o, Rose Bay, Sydney, xii.1985, D. Sheehy; 19, Eastern Suburbs, Sydney, i.1988, M. Sharon; 3♂♂, 3♀♀, Bexley, Sydney, 18.ii.1978 and iii.1983, B. Brunet; 1&, Royal National Park nr Sydney, 4.xii.1965, B. Brunet; 2♂♂, Boudi National Park, 11.i.1969, G.R. Brown; all in MSM. 6♂♂, 499, Coffs Harbour, 24,29.xii.1949, F.D.; 13, Bandon Grove, 21.xii.1958, on blackthorn bush, W.McK. Dowling; 1&, Mona Vale, 27.xii.1957, M.I.N[ikiten]; 1♀, Narrabeen, 7.i.1932, A.B.; 5♂♂, 2♀♀, Redhead, 27.xii.1925, 20–31.xii.1952, 27.xii.1955, R.D[obson]; 19, labelled only "presd by Dr Goding & Froggatt, NSW, xi.04", [also incorrectly labelled Tibicen rubra and as paratype Abricta cadulua, the latter an unpublished manuscript name]; all in MV. 1♀, Sydney, ii.1922, G.H. Hardy, QM. 19, Sydney [determined as Tibicen rubra G. & F. by Goding & Froggatt 13.10.04; also labelled as paratype of Abricta kadulua A.N. Burns but the name was never published], SAM.

#### **Description**

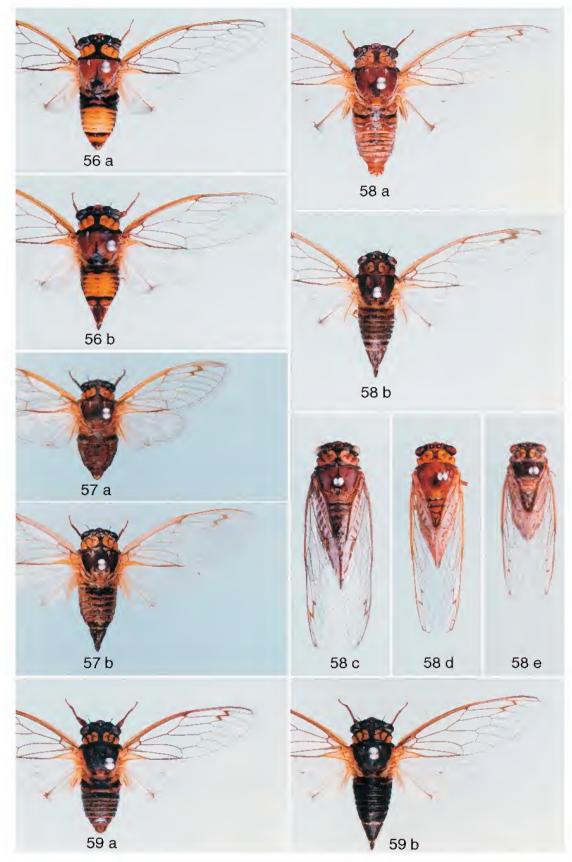
Male (Figs. 20, 46, 47, 50a,d,e,f). Head. Brown with dominant areas of black surrounding ocelli and on supra-antennal plate; usually with a muddy yellow or light brown spot on dorsal midline against posterior margin, this spot appearing as an extension of marking of similar colour along midline of pronotum. Postclypeus usually brown but often with some black, sometimes substantially black; lateral margins usually edged muddy yellow or light brown. Anteclypeus usually brown but sometimes tending black; with a small thickened anterior lip always glossy black in vicinity of midline. Rostrum brown but usually partially or entirely black in apical region, sometimes for its full length laterally; reaching to, or a little beyond, bases of hind coxae. Antennae brown to nearly black. Head usually covered to some extent with silver pubescence, especially so on underside. *Thorax*. Pronotum brown, usually of similar tone to that of head and usually paler than mesonotum (concolorous in specimens from low rainfall inland areas); midline with a broad muddy-yellow to light brown fascia terminating at or near pronotal collar, this fascia edged black, the black expanded partly along anterior margin and at its posterior end adjacent to pronotal collar; pronotal collar usually light brown, sometimes muddy-yellow, occasionally dark brown laterally anterior of lateral angle; much of pronotum usually covered to some extent with silver pubescence, sometimes extensively so except for majority of pale dorsal midline. Mesonotum usually dark ferruginous, sometimes partly black; midline usually marked by an indistinct narrow light brown fascia and a pair of similar paramedian bowed

fascia based on anterior margin and extending back to around one third the length of mesonotum; cruciform elevation with basal area light brown divided by a dark fascia along midline: usually covered to some extent by silver pubescence, sometimes substantially. Thorax below yellowish brown to dark brown. Wings. Hyaline. Fore wings always with a black infuscation at base of apical cells 2 and 3, these sometimes fused along Rs forming a single zigzag infuscation; venation usually tending black but sometimes partially brown; basal cell usually opaque amber, sometimes weakly opaque or even nearly hyaline; basal membrane muddy-vellow to black. usually a mixture of both; costal veins and most others bearing a little silver pubescence not always obvious to naked eye, this pubescence often in small dispersed clusters. Hind wings with a heavy black infuscation along full length of 2A, expanded to varying degrees along wing margin; plaga broad along basal three quarters of 3A and along much of inner margin, usually tinted brown and bordered by heavy black infuscation; usually a small black infuscation near centre of wing at base of apical cell 4; venation light brown usually with ambient vein tending black. Legs. Yellowish brown to dark brown with no distinct markings. Opercula. Muddy pale yellow narrowly edged brown or black and normally covered by fine silver pubescence; almost meeting, extending laterally beyond lateral margins of abdomen and distally a little beyond tympanal cavities. Abdomen. Tergites dark ferruginous brown to almost black; sometimes showing slightly lighter pigmentation dorsally, to a lesser extent mid-laterally and occasionally along posterior edge of tergites; an area of distinct silver pubescence laterally on tergites 2 and 3. Sternites glossy black to varying degrees with at least lateral extremities partly dark brown; sternite VIII dark brown. Tymbals (Fig. 20). As for generic description. Genitalia (Figs. 46, 47). Pygofer dark ferruginous brown; upper pygofer lobes much shorter than dorsal beak, in lateral view almost as broad as long, tending bilobed, distal end terminated at an oblique angle, in ventral view clearly lying within margins of pygofer; basal lobes with outer and inner lobes of similar length and entirely fused by a broad webbing, in lateral view outer lobe tapering to a point confluent with webbing. Uncal lobes beak-like, nearly conical and tapering to a blunt point, gently curved downwards and slightly outwards near distal end. Conjunctival claws simple, sharply pointed, directed ventrally, flattened, broad in lateral view, narrow in ventral view. A small, sublateral, gentlyrounded flange on either side of theca near distal end, visible when theca viewed ventrally or appearing as a small triangular lobe either side when theca viewed end-on. Palearis absent.

Female (Figs. 8, 50b,c). Colour and markings similar to those of male. Abdominal segment 9 dark reddish brown partly tending black on some specimens, usually very slightly paler along dorsal midline and subdorsally; dorsal beak black. Ovipositor sheath usually black or nearly so but sometimes dark reddish brown.



Figs. 52–55. Tryella species. (52) T. kauma n.sp.; a, male; b, female. (53) T. adela n.sp.; a, male; b, female. (54) T. castanea (Distant); a, c, males; b, d, e, females. (55) T. achain a n.sp.; a, male; b, female. Approx. 1.8  $\times$  natural size.



Figs. 56–59. Tryella species. (56) T. lachlani n.sp.; a, male; b, female. (57) T. graminea n.sp.; a, female; b, male. (58) T. burnsi n.sp.; a, e, males; b, c, d, females. (59) T. willsi (Distant); a, female; b, male. Approx.  $1.8 \times$  natural size.

specimens). Length of body: male 27.3-30.3 (28.9); female 31.3-34.7 (33.3). Length of fore wing: male 39.1-42.8 (40.7); female 41.5–45.4 (43.8). Width of head; male 10.2– 10.9 (10.6); female 10.4–11.8 (11.2). Width of pronotum: male 10.8–11.8 (11.3); female 11.1–12.9 (12.2). FUNNEL CREEK, SOUTH-WEST OF SARINA, CENTRAL QUEENSLAND:  $n = 10 \ \vec{\sigma} \ \vec{\sigma}$ ,  $3 \ \vec{\varphi} \ \vec{\varphi}$  (includes all available specimens). Length of body: male 21.3–24.6 (23.0); female 22.6–24.8 (23.6). Length of fore wing: male 30.2–33.3 (31.8); female 31.1– 32.6 (31.8). Width of head: male 8.3–9.0 (8.6); female 8.3– 9.1 (8.6). Width of pronotum: male 8.4–9.5 (8.9); female 8.3–9.5 (8.9). THEODORE, SOUTHEASTERN QUEENSLAND:  $n = 9 \ \delta \ \delta$ ,  $10 \$   $\$  (includes smallest and largest of available specimens). Length of body: male 23.3-25.6 (24.3); female 24.4-27.3 (26.1). Length of fore wing: male 32.1-35.2 (33.4); female 33.5–37.0 (35.2). Width of head: male 8.8– 9.3 (8.9); female 8.6–10.0 (9.3). Width of pronotum: male 8.9-9.4 (9.2); female 9.1-10.3 (9.7). LANSDOWNE, NEAR TAREE, NSW:  $n = 10 \ \vec{o} \ \vec{o}$ ,  $10 \ \vec{v} \ \vec{o}$  (includes largest and smallest of available specimens). Length of body: male 26.5–31.0 (29.0); female 28.5–36.6 (33.0). Length of fore wing: male 38.6-43.0 (41.3); female 40.2-47.9 (44.8). Width of head: male 10.3-11.3 (10.7); female 10.4-11.8 (11.3). Width of pronotum: male 10.8-12.1 (11.5); female 11.5-13.3 (12.4).

This is one of the largest species within the complex of Abricta and allied genera and is equalled only by Abricta ferruginosa from Mauritius. However, the size of specimens is markedly varied between localities, a phenomenon first noted by Moulds (1990). Individuals from areas receiving an average annual rainfall less than about 1000 mm are smaller than those from areas of high rainfall and lush vegetation (compare Kuranda and Funnel Ck measurements above). Thus, coastal specimens are usually much larger than inland specimens, except in some areas between Ayr and Bowen, and between Mackay and Rockhampton, where coastal rainfall approaches 1000 mm. Inland specimens usually have a fore wing length around 35 mm, never greater than 40 mm (note Funnel Ck and Theodore measurements). Individuals from coastal SE Qld and coastal NSW usually have a fore wing length above 40 mm (note Lansdowne measurements). Some of the largest specimens come from rainforest districts on the Atherton Tableland where a fore wing length above 43 mm is usual but length can sometimes reach over 50 mm (note Kuranda measurements).

**Distinguishing features**. The large size of this species, together with its usually pale pronotal midline and male opercula that extend laterally well beyond the body clearly characterize *curvicosta*.

Distribution (Fig. 60). Eastern Queensland and NSW from the Daintree River north of Cairns to Bendalong on the NSW South Coast. On the Atherton Tableland it is common around Julatten and Kuranda and less common around Atherton, Herberton and Ravenshoe; it also occurs in the mountains at Eungella west of Mackay, but elsewhere in Queensland it is essentially a lowland species. In central Queensland it is less common, but extends inland to the Springsure and Carnarvon Gorge. It is a common species in southeastern Queensland south from the Bundaberg district, and throughout much of its range in NSW In far southeastern Queensland it occurs inland to Inglewood. In NSW it is mainly a lowland species and is not found west

of the Great Dividing Range, although in the north of the State it has been taken inland as far as Black Swamp near Tenterfield. Throughout the species' range there are no records from localities higher than 1000 m. In both the Brisbane and Sydney regions it is widespread, often occurring in the suburbs, and it is common in some years on the eastern slopes of the Blue Mountains as high as Springwood.

Adults have been taken on the Atherton Tableland from late December to early March, in southeastern Queensland from late September to June, and around Sydney from late November to mid April. In all localities adults are usually most common during the latter half of December and in January (Moulds, 1990).

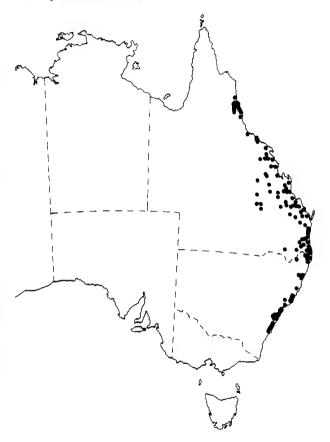


Fig. 60. Known distribution of Aleeta curvicosta (Germar).

**Habitat.** Aleeta curvicosta is associated with a wide variety of habitats and plant species but is most often found on species of the family Myrtaceae (Moulds, 1990).

**Song.** Characteristics of the song are summarized by Moulds (1990).

**Biology**. G.A. Williams (pers. comm.) has observed extensive oviposition of *Aleeta curvicosta* at his property at Lansdowne near Taree on the NSW North Coast. He maintains a small orchard adjacent to his house in a clearing bordered by both rainforest and wet sclerophyll forest. His stone fruits in particular have been heavily attacked causing considerable damage to branches which later break under fruit load. Sear damage to stems and young trunks was also prevalent. Females have been observed ovipositing on the following shrubs and trees in or near that orchard [species

marked by an asterisk (\*) have sustained moderate to heavy branch damage]: FRUIT AND NUT TREES: White Sapote, Casimiroa edulis (Rutaceae); Lime, Citrus aurantiifolia (Rutaceae); Grapefruit, Citrus×paradisi (Rutaceae); Mandarin, Citrus reticulata (Rutaceae); Orange, Citrus sinensis (Rutaceae); Macadamia, Macadamia tetraphylla (Proteaceae); Black Sapote, *Diospyros digyna* (Ebenaceae); Persimmon, Diospyros kaki (Ebenaceae); Cherimoya, Annona cherimola (Annonaceae); Guava, Psidium guajava (Myrtaceae); \*Cucumber tree, Averrhoa bilimbi (Oxalidaceae); \*Pomegranate, Punica granatum (Punicaceae); \*Apple, Malus sp. var. (Rosaceae); \*Pear, Pyrus sp. var. (Rosaceae); \*Plum, Prunus sp. var. (Rosaceae); \*Apricot, Prunus armeniaca (Rosaceae); Capulin cherry, Prunus salicifolia (Rosaceae); \*Peach, Prunus persica (Rosaceae); \*Nectarine, Prunus persica var. nucipersica (Rosaceae); Pecan, Carya illinoiensis (Juglandaceae); Almond, Prunus dulcis (Rosaceae). OTHER EXOTIC TREES AND SHRUBS: African tulip tree Spathodea campanulata (Bignoniaceae); Jacaranda, Jacaranda mimosifolia (Bignoniaceae); Yellowbells, Tecoma stans (Bignoniaceae); Buddleia, Buddleja davidii (Buddlejaceae). AUSTRALIAN NATIVES: Macadamia, Macadamia integrifolia (Proteaceae); Rhodomyrtus psidioides (Myrtaceae); Glochidion ferdinandi (Euphorbiaceae); \*Buckinghamia celsissima (Proteaceae); Stenocarpus sinuatus (Proteaceae). Oviposition has also been recorded as occurring on Lisbon lemon, Citrus limon (Rutaceae) (Anonymous, 1948).

The only known nymphal food plants are confined to native species within the Myrtaceae and include several species of *Melaleuca* (including *M. quinquenervia*) and *Callistemon* spp. which are often favoured in suburban gardens. Two native species that are favoured by adults, *Lysicarpus angustifolius* (another Myrtaceae) and *Lysiphyllum hookeri* (family Caesalpiniaceae) (Moulds, 1990; J. Moss, pers. comm.), are also very likely nymphal food plants.

Further details on oviposition and nymphal biology are given by Moulds (1990).

#### Genus Tryella n.gen.

**Type species**: *Tryella ochra* n.sp.

Included species: adela n.sp., burnsi n.sp., castanea (Distant), crassa n.sp., graminea n.sp., infuscata n.sp., kauma n.sp., lachlani n.sp., noctua (Distant), occidens n.sp., ochra n.sp., rubra (Goding & Froggatt), stalkeri (Distant), willsi (Distant).

**Etymology**. Derived from the Greek *tryelis* meaning ladle or stirrer and pertaining to the prominent ladle-like or scoop-like uncal lobes of this genus.

**Diagnosis.** Postclypeus slightly to moderately produced. Rostrum almost reaching or slightly passing hind coxae. Ocelli amber to ruby red. Width of head including eyes as wide as or slightly narrower or wider than anterior part of pronotum and as wide as or narrower than mesonotum; width of abdomen equal to that of thorax. Pronotal collar narrow with lateral angles ampliate and rounded; rudimentary and essentially confluent with adjoining sclerites anterior of lateral angles. Wings hyaline or with very weak translucent tint. Fore wing with or without infuscation;

costal margin ampliate to node, the maximum dilation greater than width of costal vein; basal cell usually with translucent pigmentation, hyaline in some species. Hind wing plaga broad along much of vein 3A plus inner margin of anal lobe, narrow along vein 2A usually to its distal end; plaga usually edged by black infuscation partly expanded along wing margin at distal end of 2A. Tymbals (Figs. 22–29) with 9–11 long ribs evenly spaced but slightly converging dorsally; basal plate small. Male opercula almost tear-drop in shape, weakly angled inwards before midpoint; nearly flat; meeting or almost meeting and extending distally to or just beyond limits of tympanal cavities. Body and basal wing veins bearing silver pubescence, varying in degree between species but most abundant on newly emerged individuals.

Male genitalia (Figs. 48–49, 67–74, 79–86, 92–101) with pygofer dorsal beak large, long and pointed; upper pygofer lobes strongly developed in most species but in some short and robust; basal pygofer lobes usually divided into a primary outer and secondary inner lobe (undivided in *occidens*), the outer lobe in lateral view either long and finger-like or substantially webbed to inner basal lobe. Uncal lobes widely separated; in ventral view somewhat scoop-like, the distal end of each upturned and cupped; in lateral view with a wing-like lateral process near base, sometimes short, sometimes long. Aedeagus in lateral view straight or gently curved for most of its length, basal plate a fused pair of nearly circular discs; conjunctival claws directed laterally or ventrally, robust, claw-like; some species with a flabellum and/or palearis.

Female abdominal segment 9 long, nearly conical; ovipositor (Figs. 9–14) long, in lateral view with modest dorsal and ventral slopes, wedge-shaped; ovipositor sheath reaching to or a little beyond apex of dorsal beak.

**Distinguishing features**. The scoop-like uncal lobes and wing-like lateral processes of the uncus are unique to *Tryella* species. *Tryella* species also differ from allied genera except *Aleeta* by having the fore wing costa strongly ampliate to node, the maximum dilation clearly wider than costal vein. The conjunctival claws at distal end of male theca are far more developed in *Tryella* than in other genera.

**Remarks**. The separation of *Tryella* from *Aleeta* (its sister group in Australia) is strongly supported both by electrophoretic data (Serkowski & Moulds, unpub. data) and the cladistic analyses. Electrophoretic data show a long genetic distance between the six *Tryella* species examined and *Aleeta curvicosta*, while cladistic analyses of morphological data show strong character support for this generic separation (Figs. 15–17). For details see Rationale for New Taxa, pp. 254–255.

**Distribution**. Mainly tropical and subtropical Australia, both coastal and inland, but also central Australia, temperate eastern Australia and southwestern Papua New Guinea.

**Habitat**. The majority of species inhabit trees and shrubs, especially Eucalyptus and other Myrtaceae. One species, *T. graminea*, is confined to grass. Adults inhabiting trees and shrubs perch along the trunks and branches, but are found most often on those with a diameter less than 50 mm.

**Biology**. In monsoonal and arid regions adults mostly emerge after heavy summer rains. Eggs are probably laid in live plant tissue but this requires confirmation.

Adults of all species tend to group together in local aggregations, those of some species even clustering on just one or several adjoining trees or shrubs. They are active both during the day and at dusk and all species, except perhaps *graminea*, are readily attracted to light. In fact the

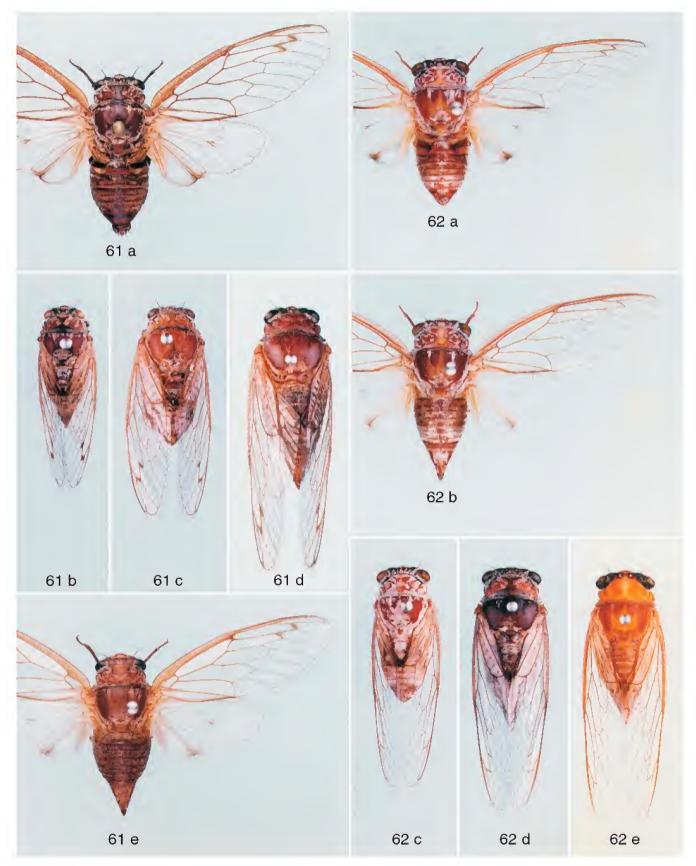
large majority of specimens in collections has been taken in this way.

Males call both during the day and at dusk. Calling males tend to aggregate and singing usually occurs in chorus.

# Key to species of Tryella

Close similarities between some species, which overlap intraspecific variation, made the task of compiling a key difficult. Consequently several species key at multiple points, although the key has been designed, as far as possible, to provide a fast determination for typical specimens. Most teneral specimens will not key correctly.

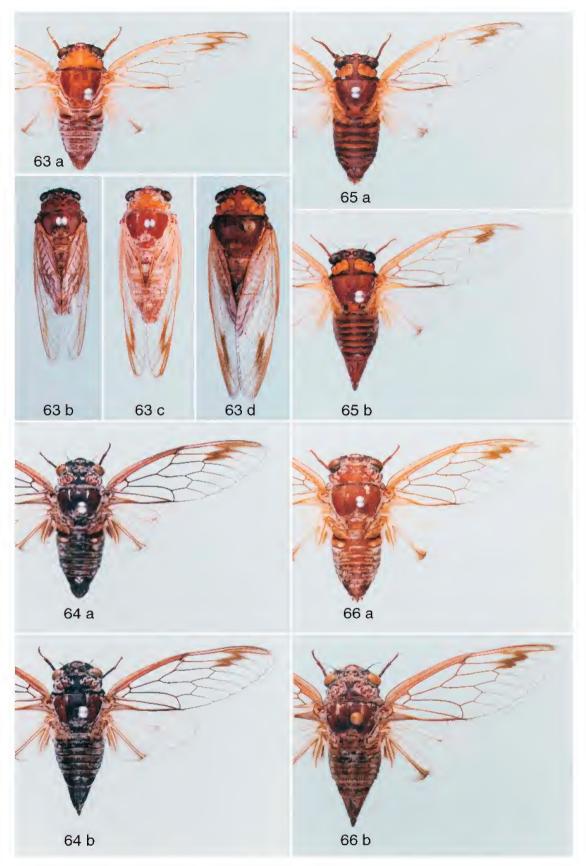
	2
- Pronotum more or less of even tone <i>or</i> with midline pale	23
Fore wing with infuscations (pigmented patches)  Fore wing without infuscations	
A black or very dark insect, the mesonotum and abdominal tergites entirely black <i>or</i> sometimes black and partly deep reddish brown, mostly on thorax	4
- Mesonotum and abdominal tergites never <i>both</i> black or nearly so	16
Fore wing with a bold infuscation that reaches to, or very nearly to, top of 3rd ulnar cell (C. Australia and inland W.A.)	5
- Fore wing with infuscation that does no approach anywhere near to top of 3rd ulnar cell (inland Qld)	willsi Distant
Postclypeus ferruginous (deep reddish brown)	occidens n.sp.
- Postclypeus black of nearly so	noctua Distant
Wings in folded position with apex of hind wing reaching, or very nearly reaching, distal end of 2nd ulnar cell	7
- Wings in folded position with apex of hind wing not reaching distal end of 2nd ulnar cell	11
Hind wing anal lobe suffused golden amber on basal ½ to ¾ (clearly visible when specimen is held 10 cm or so above a white background)	8
- Hind wing anal lobe without golden amber suffusion	
Hind wing infuscation at distal end of vein 2A small or absent, rarely extending part way along margin of anal lobe; male pygofer in lateral view (Fig. 92) with basal lobe short, upper pygofer lobe with a broad upturned pointed apex (NT & Qld)	<i>graminea</i> n.sp.
- Hind wing infuscation at distal end of vein 2A bold and usually with an obvious extension part way along margin of anal lobe; male pygofer in lateral view (Fig. 71) with basal lobe very long, slender and finger-like, upper pygofer lobe tapering to a blunt point (inland districts below the Gulf of Carpentaria both in Qld and NT).	infuscata n.sp
Fore wing with a bold infuscation (Fig. 63a) that reaches to, or	
very nearly to, distal end of 3rd ulnar cell (Pilbara region of WA)  Fore wing with infuscation that does not approach anywhere near distal end of 3rd ulnar cell (Fig. 61a)	
Pronotum (except for darkened midline) clearly paler than mesonotum; fore wing basal membrane nearly always clearly orange (E. Kimberley, monsoonal NT and lower Gulf region of Qld)	castanea Distant
- Pronotum similar in colour to mesonotum; fore wing basal membrane rarely approaching orange (atypical specimen; rarely encountered) (NT and Qld)	<i>crassa</i> n.sp.
	Fore wing with infuscations (pigmented patches)  Fore wing without infuscations



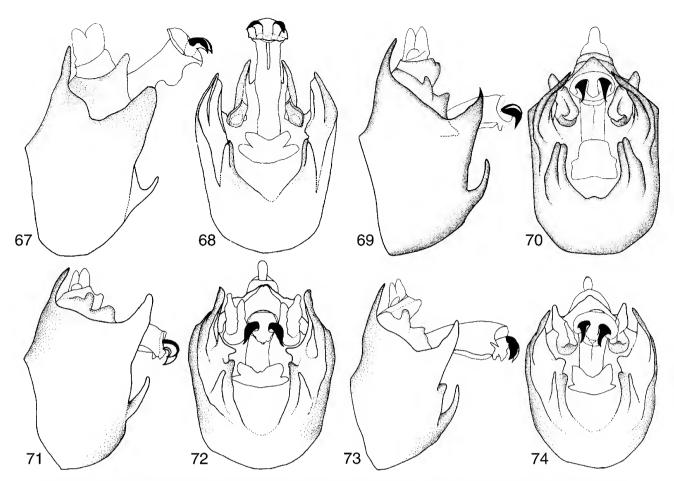
Figs. 61–62. *Tryella* species. (61) *T. crassa* n.sp.; a,c, males; b,d,e, females. (62) *T. rubra* (Goding & Froggatt); a,c, males; b,d,e, females. Approx.  $2.0 \times$  natural size.

11	Cruciform elevation black and much of abdomen dorsal side similar in colour to that of pronotum (Cape York Peninsula)  Not with above <i>combination</i> of characters	_
12	Mesonotum with a large pale area immediately anterior of cruciform elevation, never darker than remainder (Qld and lower Gulf region of NT)	ochra n.sp.
	- Mesonotum never with a pale area immediately anterior of cruciform elevation, <i>usually</i> with this area black or unicolorous	
13	Fore wing infuscation covering, or almost covering, entire basal vein of 4th apical cell (Fig. 65a) (inland districts below the Gulf of Carpentaria both in Qld and NT)	infuscata n.sp.
	- Fore wing infuscation never extending beyond base of 3rd apical cell (Fig. 58a) (3 very similar species but with distinctly different male genitalia and different geographic locations)	14
14	Male genitalia in lateral view with basal pygofer lobe very long, slender and finger-like (Fig. 83); female indistinguishable except by locality (E. Kimberley, monsoonal NT and lower Gulf region of Qld)	castanea Distant
	- Male genitalia in lateral view with basal pygofer lobe short and not like a very long thin finger (Figs. 96, 98) (Qld)	15
15	Male genitalia in ventral view with flabellum a single broad rounded lobe (Fig. 97); female indistinguishable except by locality (lower Gulf districts of Qld)	<i>kauma</i> n.sp.
	- Male genitalia in ventral view with flabellum almost divided into a pair of lobes (Fig. 99) (tropical Qld south from Iron Range)	burnsi n.sp.
16	Length of fore wing rarely below 22 mm; fore wing basal cell weakly but clearly pigmented; fore wing basal membrane orange.	17
	- Length of fore wing never reaching 22 mm; fore wing basal cell hyaline; fore wing basal membrane usually pale yellowish, crimson red, or sometimes orange	21
17	Cruciform elevation black (upper Cape York Peninsula and PNG).	
	- Cruciform elevation brown, similar in tone to remainder of mesonotum	
18	Pronotum dark reddish brown and barely paler than mesonotum (atypical specimen; rarely encountered) (Kimberley region of WA and monsoonal NT)	rubra Goding & Froggatt
	- Pronotum ochraceous and clearly paler than mesonotum	
19	Mesonotum with a large black blotch in front of cruciform elevation and front of head between eyes and base of postclypeus always brown (atypical specimen; rarely encountered) (tropical Queensland south from Iron Range)	burnsi n.sp.
	- Mesonotum usually without a black blotch in front of cruciform elevation, if present then front of head black	
20	Hind wing anal lobe usually with distinct golden amber suffusion; male genitalia in lateral view with upper pygofer lobe sharply pointed (Fig. 69); female indistinguishable except by locality (Qld and lower Gulf region of NT)	ochra n.sp.
	- Hind wing anal lobe without golden amber suffusion; male genitalia in lateral view with upper pygofer lobe rounded at apex (Fig. 83) (a specimen with atypical wing markings; rarely encountered) (E. Kimberley, monsoonal NT and lower Gulf region of Qld)	castanea Distant
		castanca Distant

21	Rostrum passing beyond bases of hind coxae but never reaching their apices (lower Gulf region of Qld)	kauma n.sp.
	- Rostrum reaching or almost reaching only bases of hind coxae (Northern Territory)	22
22	Male genitalia in lateral view with upper pygofer lobe very broad at base and tapering to a narrow rounded point (Fig. 83); basal lobe of pygofer extended into a long finger-like projection (Fig. 83); female indistinguishable (a form known only from the Victoria River, NT)  Male genitalia in lateral view with upper pygofer lobe broad and showing almost no taper to a broad blunt apex (Fig. 85); basal lobe of pygofer with projection short and gradually tapering to apex (Fig. 85) (monsoonal NT, but probably not extending W to Victoria R.)	
23	Pronotum with midline pale	-
	- Pronotum with midline dark or similar in tone to remainder	
24	Wings absolutely glass clear (not withstanding infuscations) (Kimberley region of WA and monsoonal NT)	rubra Goding & Froggatt
	- Wings weakly tinted brown, clearly visible when held above a white background (atypical specimen; rarely encountered) (NT and Qld)	crassa n.sp.
25	Fore wing with a bold infuscation that reaches to, or very nearly to, top of 3rd ulnar cell (Fig. 63a)	26
	- Fore wing either without infuscations or infuscations that do not approach anywhere near top of 3rd ulnar cell (Fig. 61a)	
26	Pronotum with a black midline (C. Aust. and inland WA)	noctua Distant
	- Pronotum with a brown midline	27
27	Hind wing plagal area along vein 3A with obvious black pigmentation (northwestern WA)	occidens n.sp.
	<ul> <li>Hind wing plagal area along vein 3A with no black pigmentation (black only along or at distal end of vein 2A) (Pilbara region of Western Australia)</li> </ul>	stalkeri Distant
28	Pronotum much paler than mesonotum	
	- Pronotum similar in colour to mesonotum	
29	Hind wing anal lobe usually with distinct golden amber suffusion; male genitalia in lateral view with upper pygofer lobe sharply pointed (Fig. 69); female indistinguishable except by locality (Qld and lower Gulf region of NT)	
	- Hind wing anal lobe without golden amber suffusion; male genitalia in lateral view with upper pygofer lobe rounded at apex (Fig. 83) (a specimen with atypical wing markings, rarely encountered) (E. Kimberley, monsoonal NT and lower Gulf region of Qld)	castanea Distant
30	Fore wing infuscation sometimes totally absent, if present wings in folded position with apex of hind wing clearly not reaching infuscation on fore wing (Kimberley region of WA and monsoonal NT)	<i>rubra</i> Distant
	- Fore wing infuscation always present; wings in folded position with apex of hind wing reaching, and usually overlapping, infuscations on fore wing	
31	Fore wing venation dark brown or black (NT and Qld)  - Fore wing venation light brown or yellowish (Pilbara region of	_
	WA)	stalkeri Distant



Figs. 63–66. *Tryella* species. (63) *T. stalkeri* (Distant); a,b,c, males; d, female. (64) *T. noctua* (Distant); a, male; b, female. (65) *T. infuscata* n.sp.; a, male; b, female. (66) *T. occidens* n.sp.; a, male; b, female. Approx. 1.7 × natural size.



Figs. 67–74. Male genitalia of *Tryella* species showing pygofer with uncus and aedeagus in right lateral view (left) and ventral view (right): (67–68) *T. stalkeri*, genitalia prep. AB50; (69–70) *T. ochra*, genitalia prep. AB7; (71–72) *T. infuscata*, genitalia prep. AB86; (73–74) *T. lachlani*, genitalia prep. AB87.

# Tryella adela n.sp.

Figs. 53a,b, 75, 85, 86

**Other material examined**. Northern Territory 2 ♂ ♂ (teneral), 1♀ (teneral), Tindal, 1–20.xii.1967, W. Vestjens; all in **ANIC**.

**Etymology**. Derived from the Greek *adelos* meaning unseen, unknown, obscure, and referring to the small size and apparent scarcity of this species.

#### **Description**

Male (Figs. 53a, 85, 86). *Head.* Usually black but sometimes brownish; often black with a pair of brown spots between lateral ocelli and eyes, and on midline against posterior margin, visible only under magnification; postclypeus and anteclypeus ferruginous. Rostrum ferruginous becoming black apically but always with extreme apex dark brown; reaching

or almost reaching bases of hind coxae. Antennae black or brown, usually with basal segment, and sometimes part of second segment, brown. Without extensive silver pubescence above but usually extensive below except on clypeus. *Thorax*. Pronotum ochraceous with a broad middorsal fascia, pale to very dark ferruginous or sometimes nearly black, this fascia spreading laterally both at its anterior end against pronotal margin to about eyes and at its posterior end against pronotal collar; pronotal collar ferruginous to nearly black but always pale anterior of lateral angles. Mesonotum ferruginous and usually very dark immediately anterior of cruciform elevation and along lateral margins above wing bases; cruciform elevation usually light brown but sometimes dark. Thorax above often lacking noticeable silver pubescence; below medium to light ferruginous and always with distinct fine silver pubescence. Wings. Hyaline. Fore wings without infuscations; venation brown, costa pale to medium ochraceous but sometimes tinted ferruginous; basal cell hyaline; basal membrane orange or orange yellow. Hind wings with a weak infuscation at the distal end of vein 2A, often extending along much of the length of 2A, sometimes also overlaying off white plaga; venation brown. Legs. Light to medium brown; without markings. Opercula. Muddy yellow, usually with narrow black edge along lateral margin; usually covered by silver pubescence not always obvious to naked eye; clearly separated exposing apex of sternite I and barely concealing tympanal cavities. Abdomen. Tergites medium to dark ferruginous, sometimes black or darkened



Fig. 75. Known distribution of Tryella adela n.sp.

on tergite 1 and anterior half of tergites 2, 3 and 8, occasionally so on 4-7. Sternites light brown, often with an irregular, broad, darkened midline that usually excludes sternite VIII. Abdomen above and below often with silver pubescence not always visible to naked eye. Tymbals. Usually 9 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 85, 86). Pygofer ferruginous; upper pygofer lobes in lateral view broad and almost straight with nearly parallel sides and a broad rounded apex, in ventral view angled slightly inwards before midpoint; basal lobes with a broad webbing fusing outer and inner lobes, in lateral view outer lobe just a short finger-like projection beyond webbing. Uncal lobes scoop-like and gently upturned at their distal ends; lateral processes of uncus in lateral view small and rounded. Conjunctival claws simple, sharply pointed, directed laterally. Flabellum produced on either side into a small triangular lobe and centrally as a low rounded lobe. Palearis absent.

**Female** (Fig. 53b). Colour and markings similar to male. Abdominal segment 9 brown, tending palest ventrally; dorsal beak usually black or nearly so. Ovipositor sheath black and clearly extending beyond dorsal beak.

**Measurements.** n =  $10 \ \delta \ \delta$ ,  $10 \ \$  (includes smallest and largest of available specimens). *Length of body*: male 12.4–13.5 (13.0); female 13.4–15.4 (14.3). *Length of fore wing*: male 16.1–18.2 (17.3); female 16.7–20.5 (18.8). *Width of head*: male 4.4–5.1 (4.9); female 4.6–5.3 (4.9). *Width of pronotum*: male 4.6–5.1 (4.9); female 4.8–5.7 (5.2).

**Distinguishing features**. Within its geographic range *T. adela* is most likely confused with *T. castanea*. Where these two species are sympatric *castanea* usually has a fore wing length greater than 22 mm, infuscations and a pigmented

basal cell. *Tryella adela* is normally smaller (fore wing length never reaching 22 mm), the fore wings are normally not infuscated and the fore wing basal cell is hyaline; male genital structures show clear differences and should be examined in doubtful cases.

Furthermore *T. adela* shows a very close resemblance to *castanea* from the Victoria River district of NT and to *T. kauma* from Queensland; *adela* differs from Victoria River *castanea* by having the fore wing basal cell hyaline instead of weakly tinted or partly tinted translucent amber, and from *kauma* by having the rostrum not passing the bases of the hind coxae and by lacking any brown on antennal plates on specimens with blackened heads.

**Distribution** (Fig. 75). Inland tropical Northern Territory where it is known from a relatively small area bordered approximately by Katherine, Bulman Aboriginal Community in south Arnhem Land and Daly Waters. Adults have been recorded only in late November and throughout December.

**Habitat.** Open woodland with shrubs. Nearly all adults have been taken at light but it is more likely that they inhabit shrubs rather than trees.

# Tryella burnsi n.sp.

Figs. 9, 22, 58a-e, 76, 98, 99

**Types.** QUEENSLAND—Holotype ♂, K179853, Morehead R. x-ing, 35 km SSE of Musgrave Hsd, Cape York Pen., 10.i.1988, M.S. & B.J. Moulds, AM. Paratypes as follows: 8♂♂, K179928-K179935, 399, K179936-K179938, Claudie R., 4 mi W Mt. Lamond, 16.xii.1971, D.K. McAlpine, G.A. Holloway & D.P. Sands; 13, K179939, Claudie R., 1 mi W Mt Lamond, 19.xii.1971, D.K. McAlpine, G.A. Holloway & D.P. Sands; 19, K179943, 2 mi S Mt Lamond, Iron Range, 17.xii.1971, D.K. McAlpine & D.P. Sands; 233, K179940 and K179944, 19, K179941, Claudie River near Mount Lamond, 4.i.1972, D.K. McAlpine & G.A. Holloway; 2 of of, K179945 and K179946, Lockhart R. Community new site, near Claudie River, 8,12.i.1972, S. Thomson; 19, K179854, same data as holotype; 1&, K179942, 12 mi N Mount Molloy, 10.xii.1971, D.K. McAlpine, G.A. Holloway & D.P. Sands; 13, K179898, Mt Molloy Airport, 25.xii.1981, A. Walford-Huggins; 1♂, K179980, Almaden, xii.1925, N.D. Campbell; 12♂♂, K179914-K179925, 299, K179926 and K179927, Speewah Rd, 5 mi S of Kuranda, 11.i.1967, D.K. McAlpine & G.A. Holloway; 13, K47518, Bowen, i.1923, E.H. Rainford; 1∂, K179855, Balnagowan, W of Mackay, 24.xii.1984, E.E. Adams; all in AM. 19, Townsville, 21.i.1958, K.L. Harley, ANIC. 3 d d (1 male genitalic preparation no. AB10), Iron Range, 2,6.i.1964, M.S. Moulds; 3 \ \ \ \ \ \ \ , Iron Range, 26.xii.1983, MBM; 1♀, Iron Range, 22.x.1976, J. North; 2♂♂, Iron Range, 26.xii.1983, G. Wood; 1♂, Claudie River, Iron Range, 18.x.1974, G. Daniels; 2♂♂, 1♀, Claudie River, Iron Range, 8,20.x.1974, M.S. Moulds; 1♂ (1 genitalic preparation no. AB4), W Claudie River. Iron Range, 25.xii.1983, MBM; 1♀, Gordon Creek, Iron Range, 16.x.1974, M.S. Moulds; 1♂, York Downs 50 km E of Weipa, 28.xii.1983, MBM; 6♂♂, 2♀♀, waterhole nr Wenlock Riv. x-ing, Portland Roads Rd, 120 m, 13°06'S 142°56'E, 1.i.1995, GAD; 13, Old Lockhart River Mission, S of Iron Range, 25.x.1974, A. Daniels; 3♂♂, [Old] Lockhart River [Mission], 12°58'S 143°30'E, 14,17.xii.1986, R.B. Lachlan; 1&, McIlwraith Rg, Leo Creek track, NE of Coen, 300 m, 2.i.1983, MBM; 1&, McIlwraith Ra, 8 km NE of Coen, 13°53'S 143°15'E, 540 m, eucalypt woodland, 8.i.1995, G. and A. Daniels; 13, Coen, 29.xii.1993, MBM; 233, 18 km S of Coen, 24.xii.1983, MBM; 1&, Barrow Point, 14°22'S 144°38'E, 13.xii.1986, R.B. Lachlan; 1♂, Little Laura River, 15 km NE of Laura, 1.i.1983, R. Storey; 1 &, 2 km S of Hann R. x-ing, 80 km NW of Laura, 15°18'S 143°53'E (gps), 29.xii.1993, MBM; 1&, 16 km SE of Hann R. x-ing, NW of Laura, 12.i.1990, MBM; 4♂♂, 2♀♀, same locality as holotype, 10.i.1988, 9.i.1990, MBM; 330. Hells Gate Creek, S of Laura, 6.7,i.1981, GAD; 2&&, 35 km SE of Laura, 23.xii.1983, MBM; 1♂, Normanby R. x-ing, 2.i.1994, 15°17'S

144°50′E (gps), MBM; 1♂, 1♀, Cooktown, 7.i.1973, M.S. Moulds; 2♂♂, Mt. Cook nr Cooktown, 31.xii.1983, MBM; 1♀, Grassy Hill, Cooktown, 21.i.1990, C. Pratt; 13, Black Mountain, S of Cooktown, 6.i.1981, MBM; 2♂♂, Black Mountain, nr Cooktown, 7.i.1992, L.R. Ring; 13, Spear Creek, 8.5 km N of Palmer River x-ing, 16°03'S 144°48'E, 26.xii.1984, GAD; 1&, McLeod River, W of Mt Carbine, 1.i.1981, MBM; 233, 19, Mt Molloy, 1,2,4.i.1974, AMW-H; 133, Rifle Creek, Mt Molloy, 9.i.1992, L.R. Ring; 2 of of, 3 km S of Mount Molloy, 16°42'S 145°20'E, 7.xii.1991, C.J. Burwell; 5♂♂ (1 male genitalic preparation no. AB59), 19, Mt Molloy airport, 25.xii.1981, A. Walford-Huggins; 19, 10 mi S of Mt Molloy, 22.xii.1973, AMW-H; 3& d (1 male genitalic preparation no. AB60), 4♀♀, Mareeba, 1.i.1983, G. Wood; 4& &, Arriga via Mareeba, 17.xi.1981, i.1990, K.H. Halfpapp; 1♀, Walsh Bluff, 17 km NW of Atherton, 30.xi.1986, D.A. Lane; 1♂, 20 km W of Atherton, 16.xi.1986, D.A. Lane; 1♀, Kuranda, 11.i.1980, G. Wood; 299, Clohesy River, Mareeba road, 28.xii.1973, AMW-H; 1&, Davies Ck, between Mareeba & Kuranda, 23.xii.1981, J. Kentwell; 1&, Trinity Beach, N of Cairns, 2.xii.1986, MBM; 1 む, Trinity Beach, N of Cairns, 5.xi.1980, J. Olive; 3 む む, 10 km N of Ellis Beach, 28,29.xii.1980, 9.i.1985, GAD; 1&, Poly Ck, nr Garradunga, Innisfail, 15.i.1990, MBM; 1♂, Wernadinga Stn, SE of Burketown, 18.xii.1986, MBM; 13, 9 km WNW of Chillagoe, 17°08'S 144°26'E, 8.xii.1991, C.J. Burwell; 4 ਹੈ ਹੈ, Chillagoe, 17°09'S 144°31′E, 8,10.xii.1991, C.J. Burwell; 1♂, 11 km WSW of Mt Surprise, 31.xii.1989, MBM; 2♂♂, 2♀♀, 24 km N of Einasleigh, 31.xii.1989, MBM; 1&, Gilbert River, W Georgetown, 4.ii.03, J. Hasenpusch; 233, Black River, nr Townsville, 4.xii.1992, T. Woodger; 1♂, 1♀, Townsville, 27.xi.1986, MBM; 3♂♂, Townsville, 18.i.1991, 27.xi.1992, 22.xii.1993, M.F. Braby; 1♀, Upper Ross [River], Thuringowa, [Townsville], 19.xii.1991, L.R. Ring; 16, St Margarets Ck, approx. 20 mi S of Townsville, 1.ii.1973, AMW-H; 4♂♂ (1 male genitalic preparation no. AB58), 1♀ 60 km SSW of Townsville, 2.ii.1981, MBM; 19, Cape R., 100 km S of Charters Towers, 21.xii.1983, MBM; 4♂♂, 1♀, Bowen, 9.xii.1990, MBM; 2♂♂, 45 km S of Collinsville, 16.i.1987, MBM; 1♀, Grassy Gully, approx. 20 km N of Proserpine, 18.i. 1975, AMW-H; 43 d, Shute Harbour nr Proserpine, 30.xii.1976, D. Lane; 1♂, Airlie Beach, Conway Rge, near Proserpine, 16.i.1984, R. Wood; 1♀, Bloomsbury, S of Proserpine, 9.xii.1980, MBM; 10, Mt Charlton, NW of Mackay, 19.i.1978, A. Hiller; 19, Landing Ck, Seaforth N of Mackay, 12.i.1986, E.E. Adams;  $5 \circlearrowleft \circlearrowleft$ ,  $5 \circlearrowleft \circlearrowleft$ , Nindavale, Mackay, 25.xii.1984, E.E. Adams; 1♂, Gargett, W of Mackay, 14.i.1979, L.R. Ring; 7♂♂, 1♀, Balnagowan, W of Mackay, 24.xii.1984, E.E. Adams; 3♂♂ (1 male genitalic preparation no. AB61),  $2 \Im \Im$ , Ilbilie Hsd, S of Mackay, 27.xii.1984, E.E. Adams; 1♂, Rockhampton, 23.i.1973, A. Atkins;  $1 \, \delta$ , Rockhampton, 26.i.1975, G.R. Brown; all in MSM.  $9 \, \delta \, \delta$ ,  $6 \, \Im \, \Im \, \delta$ Station Creek, Coen, 4.i.1959, L. W[assell], Collection A.N. Burns  $[2 \circ \circ]$  incorrectly labelled A. willsi];  $1 \circ \circ$ , Port Stewart, Cape York [Peninsula], ii.1956, L. Wassell, Collection A.N. Burns; 1 &, Nesbitt Rr, Coen, 17.xi.[19]58, L. Wassell, Collection A.N. Burns; 1♂, Massy Creek, Silver Plains, east coast Cape York Pen. 8.vii.[19]60, J.L. Wassell, Collection A.N. Burns; 233, 19, Silver Plains, Coen, 11.i.[19]59, L. W[assell], Collection A.N. Burns [1 male incorrectly labelled A. willsi]; 13, Mareeba, 31.xii.[19]50, G. B[rooks], Collection A.N. Burns; 13, Kuranda, i.[19]08, R.W. Armitage; 13, Double Is, 19.xii.[19]26, A.B., Collection A.N. Burns; 13, 19, Mowbray R, 25.i.[19]53, G. B[rooks]; Collection A.N. Burns; 1&,  $1\,^{\circ}$  , Cairns, 6.i.[19]51, 1.i.[19]53, G. B[rooks], Collection A.N. Burns; 13, Woree, 12.i.[19]26, C. Borch; 19, Hambledon, 12.ii.[19]56, G. B[rooks], Collection A.N. Burns; 1&, Meringa, 16.i.[19]25, A.N. Burns, Collection A.N. Burns; 1♂, Gordonvale, 15.i.[19]26, C. Borch; 2♀♀, Gordonvale, i.[19]30, Edmund Jarvis Coll. [incorrectly labelled A. willsi]; 1&, Aloomba, 5.i.[19]26, C. Borch; 19, Dunk Is., 31.xii.[19]49-5.i.[19]50, G. B[rooks], Collection A.N. Burns; all in MV. 3&&, Bowen, 1917, E.H. Rainford; 1♂, R'hampton [=Rockhampton], 1937, S.R. Brock; 1♀, Nindavale, Mackay, 25.xii.1984, E.E. Adams; all in QM. 9♂♂, 17♀♀, Flinders I., i.1927, Hale & Tindale; 1♂, Townsville, xii.[19]03, F.P. Dodd; 13, 19, Bowen, 1917, E.H. Rainford; all in SAM. 333, West Claudie River, 4.5 km SW road junction, 12°44'S 143°15'E, 3,5.xii.1986, G. Daniels M. Schneider; 1♂, Meringa, 1.i.[19]47, J. Losser; 1♂, Meringa, 4.i.[19]26, C.B.; 1♂, Mackay, ii.1964, J.E. Dunwoody; all in UQIC.

Other material examined. QUEENSLAND—1♀, K56227, Almaden, Chillagoe Dist., iv.1927, W.D. Campbell; 1♀, K66716, Saddleback Is., off Pt. Denison, xii.1932, F.A. McNeill; all in AM. 1♀, Pine Ck, 21.i.1962, Carne & Britton; 1♂, Station Creek, Coen, 4.i.1959, L.

W[assell]; 2♀♀, Endeavour River, W.W. Froggatt Collection; 1♀, Pt Douglas, 17.i.1962, Carne & Britton; 19, Annan River, Cooktown, 1965, Brown; 1&, Cairns, Jarvis, W.W. Froggatt Collection; 1&, Cairns, i.190[?], Abricta willsi, Dist. W.W. Froggatt Collection; 1 ♂, Deeral, 19[??], J.F. Illingworth Coll., Abricta kurandae, Cairns, Coll. & det. W.W. Froggatt; 2♂♂, Palm Island, M.J. Mackerras; all in ANIC. 1♂, B.M. 1907-54, F.P. Dodd (no other data), BMNH. 19, Rifle Creek, Mt Molloy, 9.i.1992, L.R. Ring (teneral); 13, 18 km W of Hells Gate roadhouse [W of Burketown], 20.xii.1991, MBM; both in MSM. 13, Claudie R., ii.[19]14, Dr Macgillivray; 26 d, Cairns, 17, J.F. Illingworth Collection; 13, Cairns dist, A.M. Lea, incorrectly labelled Abricta castanea; 2♂♂, Meringa, 2.i.[19]26, A.N. Burns, Collection A.N. Burns; 1 of, Meringa, C. Borch; 2 of of, Gordonvale, 15.i.[19]26, C. Borch; 2♂ ♂, Gordonvale, 22.i.[19]19, E. Jarvis; 1♀, Gordonvale, i.[19]30, Edmund Jarvis Coll. [incorrectly labelled A. willsi]; 19, Mackay, H.W. Brown; all in MV. 1♂, Cairns, J.F. Illingworth; 1♀, Deeral, J.F. Illingworth [incorrectly det. as *Tibicen kurandae*], both in **QM**. 299, Greta Ck, 20 mi N of Proserpine, 1.i.1965, G. Monteith, both in UQIC. 5 \$\displaystyle 5 \displaystyle 5 \displayst incorrectly labelled Abricta willsii); 13, 19, Stanley I., Flinders I. [Group], i.1927, Hale & Tindale; 5♂♂, 2♀♀, Cairns dist., A.M. Lea (1♀ incorrectly labelled Abricta willsii, 1♂ incorrectly labelled both Abricta castanea and Abricta willsii); 1 &, Deeral, J.F. Illingworth (incorrectly labelled Tibicen kurandae); all in SAM.

**Etymology**. Named in honour of Alex Burns who wrote a number of papers on Australian cicadas and once intended to revise the genus *Abricta*.

### **Description**

Male (Figs. 22, 58a,e, 98, 99). Head. Ferruginous and black in variable proportions; always black below and adjacent to ocelli and eyes; postclypeus, anteclypeus and most anterior part of head between eyes and postclypeus always brown. Rostrum ferruginous becoming black apically; reaching beyond bases of hind coxae but not extending to their apices. Eyes of live specimens blood red, variable in intensity. Antennae usually black but sometimes tending brown; basal segment always brown. Usually without obvious silver pubescence above but nearly always present below, principally on maxillary plates. *Thorax*. Pronotum ochraceous with a broad light to dark ferruginous or black middorsal fascia, this fascia spreading laterally both at its anterior end against pronotal margin as far as eyes, and at its posterior end against pronotal collar where it is always pale, or partly so (this pale area clear under magnification); pronotal collar black and ferruginous to varying degrees but always ochraceous laterally anterior of lateral angles. Mesonotum ferruginous and nearly always with a diffuse black blotch immediately anterior of cruciform elevation and along lower lateral margin above wing bases: sometimes with a pair of middorsal obconical markings distinguishable, their bases on anterior margin; cruciform elevation light brown. Thorax above usually without silver pubescence. Thorax below a mixture of ferruginous and black and always with fine silver pubescence. Wings. Hyaline. Fore wings usually with distinct infuscations at apex of apical cell 1, the base of apical cell 2 and the basal cross veins of apical cell 3; the degree of infuscation variable from bold, which often fills much of apical cell 1, to substantially reduced and limited to just the basal cross veins of cells 2 and 3 and apex of cell 1, and in rare extreme case completely lacking; venation brown, sometimes nearly black, costa ochraceous; basal cell weakly tinted translucent amber; basal membrane orange; costa and veins on basal third or so occasionally bearing some silver pubescence not visible to naked eye. Hind wings with a distinct infuscation at distal end of vein 2A which sometimes extends partially around margin of anal lobe no further than 3A; sometimes also infuscated on basal half of anal lobe especially in plagal region, otherwise anal lobe weakly tinted translucent amber clearest on basal half; plaga off white, often contaminated by black; venation brown. Legs. Medium to light brown; without markings. Opercula. Muddy yellow to light orange brown, sometimes with black at extreme base and along lateral margin; clearly separated exposing apex of sternite I and barely concealing tympanal cavities; usually covered by silver pubescence not always obvious to naked eye. Abdomen. Tergite 1 black; tergites 2–7 light orange brown to ferruginous with a black anterior margin that is broadest across dorsal region; tergites 3-7 also usually with a very narrow pale yellowish posterior margin; tergite 8 black on basal half or so, remainder orange brown. Sternites medium to light brown, often with posterior margins of III-VI with a narrow pale yellow posterior margin. Abdomen above and below often with silver pubescence not always obvious to naked eye. Tymbals (Fig. 22). Usually 10-11 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 98, 99). Pygofer orange brown to ferruginous tending dark around upper pygofer lobes, yellowish at outer basal lobe; upper pygofer lobes in lateral view broad, upper margin distinctly curved outwards in central region, lower margin straight, distal end curved upwards towards an upturned pointed apex, in ventral view angled slightly inwards; basal lobes with a broad webbing fusing much of outer and inner lobes, in lateral view outer lobe just a short finger-like projection beyond webbing. Uncal lobes scoop-like and gently upturned at their distal ends; lateral processes of uncus in lateral view nearly equal in length to upper pygofer lobes, angled slightly upwards from near base and bluntly terminated. Conjunctival claws simple, sharply pointed, directed laterally. Flabellum present ventrally, produced on either side into a rounded lobe. Palearis absent.

**Female** (Figs. 9, 58b–d). Colour and markings similar to male. Abdominal segment 9 ferruginous brown paling ventrally. Ovipositor sheath black and clearly extending beyond dorsal beak.

**Measurements.** n = 10 ♂ ♂, 10 ♀ ♀ (includes smallest and largest of available specimens). *Length of body*: male 14.8–18.1 (16.7); female 18.1–22.5 (19.7). *Length of fore wing*: male 20.1–25.0 (22.8); female 22.7–27.4 (24.7). *Width of head*: male 5.5–6.5 (6.1); female 6.0–6.8 (6.3). *Width of pronotum*: male 5.7–7.0 (6.4); female 6.2–7.2 (6.7).

**Distinguishing features**. The exceptional variation in fore wing infuscations, and the close similarity of this species with others, calls for care in identification. Some individuals of *T. burnsi* are almost indistinguishable from some individuals of *castanea*; however the distributions of these two species are quite distinct (ignoring the doubtful record from near Burketown) and specimens of known origin are easily determined. There are also clear differences in male genitalia, primarily in the shapes of the upper and lower pygofer lobes.

Confusion of *burnsi* with *T. kauma* is also a possibility although their distributions probably do not overlap. Where doubt of identity exists male genitalia should be examined; the conjunctival claws in ventral view are strongly recurved in *kauma* while the flabellum of *burnsi* is clearly separated into a pair of lateral lobes.



Fig. 76. Known distribution of *Tryella burnsi* n.sp. Localities bearing a question mark require confirmation (see text).

Atypical specimens of *burnsi* without fore wing infuscations could be mistaken for *T. ochra* but the presence of a large black blotch anterior of cruciform elevation in *burnsi* clearly separates specimens of *burnsi* from those of *ochra* which are pale immediately anterior of cruciform elevation or evenly coloured.

**Distribution** (Fig. 76). Tropical and subtropical Queensland south from Weipa and Iron Range to Rockhampton. Nearly all records are from along the east coast with a small number of inland records extending west as far as the Gilbert River and possibly to the Cape River. A single male taken west of Burketown appears to be this species but in view of its isolation is treated as doubtful until further specimens are obtained to confirm its identity. Likewise, the Cape River record is based upon a single female, the identity of which also requires confirmation.

Usually populations tend to be small but occasionally the species is locally common. Adults have been taken from October to early February, with single records for April and July. They are most abundant during December. This species may be sympatric with *willsi*. The known distributions of these two species are, for the most part, allopatric but they may be possibly sympatric in coastal districts between Mackay and Rockhampton although all known records for the two species in this region are separated by the Connors Range, *willsi* occurring only to the west and *burnsi* only to the east.

**Habitat.** Probably eucalypt trees and saplings, where adults favour the smaller branches.

# Tryella castanea (Distant, 1905), n.comb.

Figs. 10, 54a-e, 77, 83, 84

Abricta castanea Distant, 1905a: 27; Distant, 1906: 131; Kirkaldy, 1907a: 16; Ashton, 1914: 349; Kato, 1932: 181; Burns, 1957: 635; Metcalf, 1963: 206; Duffels & van der Laan, 1985: 234; Moulds, 1990: 122–123; Ewart, 1993: 139.

**Types.** Syntype series of  $5\ \cdot \cdo$ 

Distant (1905a) did not designate a holotype or state the number of specimens examined. He did, however, indicate in his description that he had several specimens and gave a range for male body length. All six specimens in BMNH listed above that are believed to be syntypes are considered conspecific.

Type locality. Distant (1905a) gave the type locality simply as "North Australia" and the collector as "J.R. Elsey". The description of castanea states "tegmina unspotted" and indeed the type series totally lacks fore wing infuscations except for one male with some very limited infuscation. Specimens consistently lacking fore wing infuscations, or occasionally with very limited infuscation, are known only from the Victoria River, Northern Territory, especially from the vicinity of Timber Creek township (see comments below). These also tend to be smaller than specimens from elsewhere and the syntype series clearly falls within this smaller size range. Further, Distant (1905b) described Abricta elseyi from the Victoria River, from material taken by Dr J.R. Elsey during the Gregory Exploration Expedition, British Museum, As J.R. Elsev is also stated to be the collector of the type series of castanea it is reasonable to conclude that the type locality of this species is also the Victoria River.

**Material examined**. Western Australia—1♂, K179957, 1♀, K179956, Fitzroy & Margaret Rs, 1896, Calvert Exped., H. Ashton Coll.; 1♂, K179847, Wyndham, 31.xii.1991, MBM; 1♀, K179848, Kununurra, 7.i.1986, MBM; all in AM. 13, Wyndham-K.R.S. [Kimberley Research Station], 15.x.1953, R. Lukins; 13 (genitalic preparation no. AB101), Forrest R. Mission, 7.i.1954, R. Lukins; 16, 1♀, Wyndham, 27.i, 29.iii, 25.iv.1930, T.G. Campbell; 2♂♂, 1♀, Wyndham, 26.xii.1930, 5.xii.1930-8.i.1931, H.J. Willings; 4 of of (1 male genitalic preparation no. AB90), 19, Ascot Station, Wyndham, 14.i.1930, T.G. Campbell; all in ANIC. 1♀, Tunnel Creek, E of Derby, 1.xi.1978, MBM; 1♂, 16 km NW of Fitzroy Crossing, 1.i.1986, MBM; 10♂♂, 1♀, 50 km SSE of Fitzroy Crossing, 1.i.1986, MBM; 3♂♂ (two male genitalic preparations Nos AB17, AB70), 19, 80 km SW of Halls Creek township, 2.i.1986, MBM; 2♂♂ (one male genitalic preparation no. AB63), Halls Creek township, 2.i.1986, MBM; 23 3, 299, 11 km S of Turkey Creek township, 3.i.1986, MBM; 1♂, Little McPhees Ck, 150 km S of Wyndham, 3.i.1986, MBM; 1♂ (genitalic preparation no. AB95), Zebidee Springs, El Questro Stn, E Kimberley, 28.xii.1991, MBM; 5♂♂, 3♀♀, Wyndham, 4.i.1986, 31.xii.1991, MBM; 13, 20 km W of Ord River, Duncan Hwy, 3.i.1986, MBM; 333 (one male genitalic preparation no. AB64), 399, Kununurra, 7.i.1986, MBM;  $2 \stackrel{\circ}{\circ} \stackrel{\circ}{\circ}$  (one male genitalic preparation no. AB75),  $1 \stackrel{\circ}{\circ}$ , Kununurra, 28.i.1987, E.A. Henty; all in MSM. 933, 299, Forrest R. Mission, ii.1954, 6,9.i.54, K.J.C., Collection A.N. Burns; 1♂, Kimberley Res Stn, Wyndham, 10.xii.[19]53, G. Lukins, Collection A.N. Burns; 1 \, Wyndham, 23.xii.1953, R. Lukins, Collection A.N. Burns; all in

MV. 13, Calvert Exped., 1896, Fitzroy & Margaret Rs. (no other data), in SAM. NORTHERN TERRITORY—1∂, K179849, 1♀, K179850, Victoria Hwy, Dingo Ck, nr W.A. border, 1.i.1992, MBM; 1♂, K179852, 1♀, K179851, Victoria R. 18 km W of Timber Creek township, 25.xii.1991, MBM; 2♂♂, K179947 and K179950, 2♀♀, K179948 and K179949, Zimmin Rd, Katherine, 6,17.xii.1996, ex Citrus limon, M. Hoult: 19. K179951, 20 mi NE Oenpelli, x.1970, W. Omer-Cooper; 4♂♂, K179952-K179955, Wa Wee Billabong area, 8,10,11.x.1970, W. Omer-Cooper; all in AM. 19, 30 mi[les] SE of Adelaide River (town), 1.xi.1966, A. & R. Mesa; 6♀♀, Tindal, 14°31'S 132°22'E, 1–20.xii.1967, light trap, W.J.M. Vestjens; 2♂♂, 3♀♀, Katherine, 27.xi.1967, W.J.M. Vestjens; 1♂, 16°18'S 133°26'E, 9 km SSE of Daly Waters, 11.xi.1979, T. Weir; 1♀, Tennant Creek, 1906, Field, W.W. Froggatt Collection; all in ANIC. 14 $\delta \delta$  (one male genitalic preparation no. AB97),  $14 \circ \circ$ , Victoria Hwy, Dingo Ck, nr W.A. border, 1.i.1992, MBM; 6 ♂ ♂ (one male genitalic preparation no. AB69), 2♀♀, junct Victoria & Duncan Hwys, E of Kununurra, 6.i.1986, MBM; 1&, Victoria Hwy, 110 km E of Kununurra, 26.xii.1991, MBM; 1&, Alpha Ck, 35 km W of Timber Creek township, 8.i.1986, MBM; 35 & d (2 & d genitalic preparations Nos AB96, AB99), 18♀♀ Victoria R. 18 km W of Timber Creek township, 25.xii.1991, MBM; 2 of of (male genitalic preparations Nos AB13, AB68), 19, 40 km E of Timber Creek, Victoria Hwy, 8.i.1986; 22 ♂ ♂ (one male genitalic preparation no. AB98), 22 ♀ ♀, Victoria Hwy, 10 km E of Victoria R. Inn, at river x-ing, 2.i.1992, MBM; 1♀, Dashwood x-ing, Victoria R., nr Victoria R. Downs, 24.xii.1991, MBM; 2♂♂ (one male genitalic preparation no. AB62), 6♀♀, Springvale Stn, 12 km W of Katherine, 8.xii.1982, A. Walford-Huggins; 42 o o (2 male genitalic preparations Nos AB14, AB15), 44 \, \, \, Waterhouse River, Mataranka Hsd, 9.i.1986, 23,24,25.xii.1986, MBM; 3♂♂, 6♀♀ 38 km N of Daly Waters, Stuart Hwy, 23.xii.1986, MBM; 1♂, 1♀, 32 km N of Daly Waters, Stuart Hwy, 23.xii.1986, MBM; 1&, 25 km N of Daly Waters, 23.xii.1986, MBM; 2♀♀, 10 km N of Daly Waters, 8.xii.1982, A. Walford-Huggins; 13, 11 km N of Dunmarra, Stuart Hwy, 23.xii.1986, MBM; 1♂, Elliott, 7.xii.1982, A. Walford-Huggins; 123 ♂ (one male genitalic preparation no. AB16), 7♀♀, Tennant Creek township, 23.i.1977, 22.i.1984, MBM; 1&, Borroloola, 22.xii.1991, MBM; 13 (genitalic preparation no. AB72), 70 km S of junction Carpentaria/Tablelands Hwys, 12.i.1986, MBM; all in MSM. 2♀♀, Katherine, xii.1957, J. Wren, Collection A.N. Burns; 3♀♀, Katherine, xii.1959, B.W. Wren, Collection A.N. Burns, (1 labelled holotype, 2 labelled paratypes of A. tacomona, an unpublished manuscript name); all in MV. 1 $^{\circ}$ , Daly R., (no date), H. Wesselman;  $3 \stackrel{\circ}{\circ} \stackrel{\circ}{\circ}$ ,  $2 \stackrel{\circ}{\circ} \stackrel{\circ}{\circ}$ , Tennant's Ck., (no date), J.F. Field (1♂, 1♀, incorrectly labelled Abricta willsi); all in SAM. 19, Auvergne Stn, 4.xii.1965, J. Edey, in UQIC. QUEENSLAND-13, Escott Stn, W of Burketown, 17°44'S 139°25'E, 19.xii.1991, MBM, in MSM.

#### Description

Male (Figs. 54a,c, 83, 84). Head. Usually black and ferruginous in variable proportions with the black dominant, but some individuals entirely brown or almost so; antennal plate nearly always partly or entirely ferruginous; postclypeus and anteclypeus ferruginous. Rostrum ferruginous becoming black apically, reaching to about bases of hind coxae. Eyes of live specimens (Victoria River, NT) initially light grey becoming dark grey and finally black with maturity. Antennae usually black but sometimes tending brown; basal segment always brown and usually also part of second segment. Without obvious silver pubescence above but usually distinct below except on clypeus. Thorax. Pronotum ochraceous with a broad pale to very dark ferruginous fascia on midline, this fascia spreading laterally both at its anterior end against pronotal margin to eyes or sometimes beyond, and at its posterior end against pronotal collar; on some individuals the inner portion of this middorsal fascia is very pale so that the fascia appears in outline only while on some other individuals the expansion against the pronotal collar is paler than remainder; pronotal collar either entirely black, entirely ferruginous, or a mixture of both. Mesonotum light to dark ferruginous, sometimes with a pair of middorsal

obconical markings based on anterior margin partially or totally defined; cruciform elevation often light brown but always darkened to varying degrees in dark specimens. Thorax above usually without noticeable silver pubescence. Thorax below medium to light brown and always with fine silver pubescence. Wings. Hyaline. Fore wings either without infuscations or with infuscations confined to bases of apical cell 2 and the basal cross vein of apical cell 3, usually infuscation is confined to the cross veins of both cells only but sometimes the infuscation joins along Rs: venation brown, sometimes black basally, costa ochraceous; basal cell weakly tinted translucent amber; basal membrane orange; costa and veins on basal third or so occasionally bearing some silver pubescence not visible to naked eye. Hind wings with a distinct infuscation at distal end of vein 2A which sometimes extends partially around margin of anal lobe no further than 3A, and sometimes overlaying off white plaga; venation brown. Legs. Medium to light brown; without markings. Opercula. Muddy yellow suffused black to varying degrees between individuals, sometimes nearly black; usually covered by silver pubescence not always obvious to naked eye; clearly separated exposing apex of sternite I and barely concealing tympanal cavities. Abdomen. Tergites medium to dark ferruginous, sometimes nearly black, with little tonal variation within individuals although there is a tendency on some specimens for posterior half of each segment to be slightly paler. Sternites somewhat similar in colour but tending on some specimens to be pale on posterior half of sternites III-VI. Abdomen above and below often with silver pubescence not always visible to naked eye. Tymbals. Usually 10 long tymbal ribs, smaller specimens often with 9, otherwise as for generic description. Genitalia (Figs. 83, 84). Pygofer dark ferruginous; upper pygofer lobes in lateral view very broad at base tapering to a narrow rounded apex, in ventral view nearly straight and usually tilted slightly inwards; basal lobes without webbing fusing inner secondary lobes and outer lobes, outer lobes in lateral view like a very long thin finger, gently curved, nearly equal in length to upper pygofer lobes. Uncal lobes scoop-like and gently upturned at their distal ends; lateral processes of uncus in lateral view nearly equal in length to upper pygofer lobes, often slightly curved downwards and broadly rounded at apex. Conjunctival claws directed laterally, the distal end of each bearing three sharply-pointed teeth, the central tooth longest. Flabellum absent. Palearis absent. Usually ventral surface of theca with small raised transverse ridges widely spaced.

**Female** (Figs. 10, 54b,d,e). Colour and markings similar to male. Abdominal segment 9 light to very dark ferruginous; dorsal beak usually black or blackish. Ovipositor sheath black and clearly extending beyond dorsal beak.

**Measurements.** 10 km E of Victoria River Inn, NT: n =  $10 \ \delta$ ,  $10 \ \$ 9 (includes smallest and largest of available specimens). *Length of body*: male 11.3–15.3 (13.6); female 13.5–17.0 (15.0). *Length of fore wing*: male 16.8–20.0 (18.5); female 18.4–21.6 (20.0). *Width of head*: male 4.4–5.8 (5.1); female 4.8–6.0 (5.4). *Width of pronotum*: male 4.4–5.5 (5.0); female 4.8–6.3 (5.5). MATARANKA HOMESTEAD, NT: n =  $10 \ \delta$   $\delta$ ,  $10 \$ 9 (includes smallest and largest of available specimens). *Length of body*: male 14.6–17.3 (16.0); female 15.4–18.7 (17.4). *Length of fore wing*: male

19.1–22.5 (21.2); female 20.5–23.8 (22.4). Width of head: male 5.1–5.9 (5.5); female 5.3–6.0 (5.9). Width of pronotum: male 5.1–6.2 (5.7); female 5.5–6.5 (6.2). TENNANT CREEK TOWNSHIP, NT:  $n = 10 \ \cdot \cdo$ 

Adult variability. There are marked size differences both within and between populations with those from lower rainfall regions usually smaller than those from areas of high rainfall and lush vegetation. Specimens from the Victoria River catchment are characteristically small (compare measurements above). Typical of the majority of localities are those from Mataranka Homestead (with a fore wing length from 19–24 mm). The specimens from Tennant Creek are possibly abnormally large as they were taken from lush eucalypts in watered parkland.

Tryella castanea is the most variable of all Tryella species, not only in size (see above) but also in colour and fore wing infuscations. Colour differences may be partially due to aging with darker individuals being older. The presence of fore wing infuscations is characteristic for most localities throughout the species' range although there is some variability, but never is infuscation exceptionally bold with confinement to the base of apical cells 2 and 3 and nearly always to the cross veins only; a lack of fore wing infuscation is typical only for specimens from near the Victoria River (near Timber Creek township and Victoria River Inn) although a small percentage (approximately 10%, n=102) do show weak infuscations.

Electrophoretic examination of populations from Wyndham in Western Australia, Dingo Creek, Timber Creek and Victoria River Inn in Northern Territory and Escott Station in Queensland that displayed considerable differences in size, colour and wing infuscation, confirmed all were conspecific (Serkowski & Moulds, unpub. data); all possess male genital structures typical of *castanea*. Further, the population from Timber Creek which included individuals with either black or grey eyes were clearly shown to be homogeneous.

**Distinguishing features.** The exceptional variability of this species calls for care in identification. Within the geographic range of *castanea* the most similar species is T. adela. However, where the two are sympatric (central and eastern part of monsoonal Northern Territory), only small atypical specimens of *castanea* are likely to be confused with adela. Typical specimens of castanea differ not only in their normally larger size (fore wing rarely below 22) mm), but also by having the basal cell pigmented and the antennal plate nearly always brown rather than black (visible under magnification); male genital structures show clear differences between castanea and adela and should be examined in doubtful cases. For the most part, however, castanea is not sympatric with adela and geographic location usually provides an excellent guide to identity. Some individuals of T. castanea are almost indistinguishable from some individuals of T. burnsi (except for male genitalia); however, the distributions of these two species are quite distinct (ignoring a doubtful record from near Burketown) and specimens of known origins are easily determined.

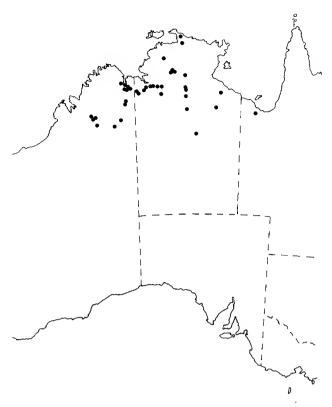


Fig. 77. Known distribution of Tryella castanea (Distant).

**Distribution** (Fig. 77). Kimberley region of Western Australia, northern half of Northern Territory where records are concentrated on the Victoria River region and along the Stuart Highway between Adelaide River and Tennant Creek with additional isolated records from western Arnhem Land, 70 km south of junction of Carpentaria/Tablelands Highways and Borroloola, and from far northwestern Queensland near Burketown. Records are lacking from the interior of the Kimberley region, the Tanami Desert and much of Arnhem Land but these absences almost certainly reflect a lack of collecting rather than a true absence from these areas.

Adult emergence is probably dependent upon wet season rains. There are records from October to late April.

The distribution for this species given by Moulds (1990) includes records of other *Tryella* species unrecognized at the time as distinct from *T. castanea*.

**Habitat**. Adults appear to favour small branches amongst tree foliage.

**Song.** Singing occurs both during the day and at dusk although the dusk song is usually by far most vigorous and sustained. An analysis of the song is under study (Moulds, in prep.).

**Biology**. Adults emerge after dark and are capable of flight even before their wings harden. They are pale straw coloured on emergence but show signs of their final pigmentation within 2 hours and are fully coloured and ready to sing by morning.

Severe damage to lemon trees, *Citrus limon*, in an orchard near Katherine, NT was caused by large numbers of adults ovipositing in semi-hardened flush growth (R. Dodd, pers. comm.).

# Tryella crassa n.sp.

Figs. 23, 61a-e, 78, 81, 82

**Types**. Holotype ♂, K179830, 16 km E of Cloncurry, N Queensland, 19.i.1984, M.S. & B.J. Moulds; in AM. Paratypes as follows: NORTHERN TERRITORY— $2 \delta \delta$ , K179831 and K179833,  $1 \circ$ , K179832, Kalkaringi, 17°26'54"S 130°50'05"E (gps), 10.i.2001, MBM; all in AM. 19, Kalkaringi, 17°26'54"S 130°50'05"E (gps), 10.i.2001, MBM, in **BMNH**. 16♂♂, 10♀♀, Kalkaringi, 17°26'54"S 130°50'05"E (GPS), 10.i.2001, MBM; 1♂, 123 km SW of Kalkaringi, 17°45'48"S 129°52'10"E (gps), 10.i.2001, MBM; 13 (genitalic preparation no. AB45), 80 km SW of Katherine, 6.ii.1977, MBM; 3♂♂ (one male genitalic preparation no. AB89), 2♀♀, Mataranka Hstd, 11.i.1992, MBM; all in MSM. QUEENSLAND—16, same data as holotype and allotype, ANIC. 13, same data as holotype and allotype, in BMNH. 833, 15 km E of Mt Surprise, 2.iii.1998, J. Olive and J. Thompson; all in **JO**. 633 (one male genitalic preparation no. AB46), 3 ♀ ♀, Lawn Hill Ck, Adels Grove, W of Gregory Downs, 19.xii.1986, 18.xii.1991, MBM; 2♂♂, 1♀, Normanton, 15.i.1986, MBM; 18♂♂ (one male genitalic preparation no. AB25); 499, same data as holotype; 633, 399, 20 km W of Cloncurry, 20.i.1984, MBM; 3&&, Selwyn Mine, 160 km SE of Mt Isa, 21.ii.1991, 26.i.1995, 30.i.1997, T. Woodger; 12♂♂, 3♀♀, 40 km W of Georgetown, 16.i.1992, MBM; 11♂♂ (one male genitalic preparation no. AB9), 499, Bruce Hwy, nr Salt Water Ck, 20 km S of Home Hill, 22.xii.1987, MBM; all in MSM. 13, 19, same data as holotype and allotype, both in QM.

**Etymology**. From the Latin *crassus* meaning thick, fat or stout and pertaining to the stocky build of this species.

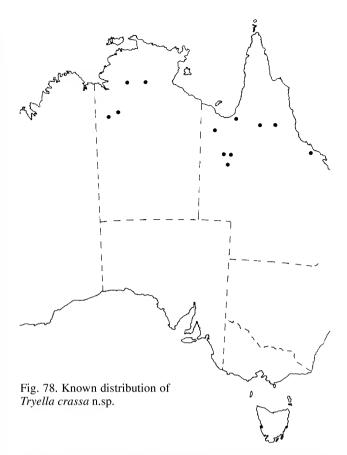
#### Description

Male (Figs. 23, 61a,c, 81, 82). Head. Dark ferruginous usually partly tending black and usually a little darker than thorax, occasionally almost entirely black except for postclypeus; postclypeus always ferruginous brown and usually lighter in tone than thorax; anteclypeus ferruginous brown to nearly black but usually with midline entirely or partly of a lighter tone. Rostrum brown and black to varying degrees but usually brown basally becoming black towards apex and often with extreme apex brown; not quite reaching bases of hind coxae. Eyes of live specimens light grey with no distinct pseudopupil. Antennal plates well developed and when viewed from directly in front covers most of antennal segment 1. Antennae usually black but sometimes partly brown. Often bearing some silver pubescence most obvious below. Thorax. Pronotum dark reddish brown to dark ferruginous, usually unicolorous but on some individuals midline marginally darker or paler; pronotal collar usually a little darker than remainder, sometimes tending blackish. Mesonotum similar in colour to pronotum; virtually concolorous but some individuals with a very faint obconical marking each side of midline against anterior margin. Thorax above often bearing a little silver pubescence. Thorax below similar in colour to above and nearly always with an obvious covering of silver pubescence. Wings. Hyaline but usually with a faint brown suffusion. Fore wings infuscated at bases of apical cells 2 and 3, usually appearing as a continuous zigzag but sometimes as two spots confined to crossveins; some individuals also infuscated at apical cell 1 partly or entirely along length of vein R1b; venation brown, costa light yellowish brown; basal cell tinted brown, usually darker than tint on remainder of the wing; basal membrane light yellowish brown; lacking silver pubescence obvious to naked eye. Hind wings with a distinct infuscation at distal end of vein 2A which sometimes extends partially around margin of anal lobe; often a small infuscation near centre of wing at base of apical cell 4; basal half or so of anal lobe weakly tinted brown similar to the tint of fore wing basal cell; plaga off-white; venation from light brownish vellow to brown. Legs. Dark reddish brown to dark ferruginous, similar in tone to that of thorax; without noticeable markings. Opercula. Pale muddy yellow to dark brown tending black; often bearing some fine silver pubescence usually discernible to the naked eye; clearly separated exposing apex of sternite I and barely concealing tympanal cavities. Abdomen. Tergites dark reddish brown to dark ferruginous, similar in tone to that of thorax; tergite 8 usually with its posterior margin narrowly edged black at least across dorsal half. Sternites variable between individuals, sometimes entirely brown, sometimes with pale posterior margins and sometimes with black posterior margins, the distal half or so of sternite VII nearly always dark. Abdomen above and below often with some fine golden pubescence. Tymbals (Fig. 23). Usually 10 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 81, 82). Pygofer dark reddish brown to dark ferruginous; upper pygofer lobes in lateral view clearly subdivided with a large, broad, rounded basal section behind which continues an apical section that tapers to a blunt rounded point, in ventral view tilted slightly inwards with the subdivision of terminal sections clearly visible externally as a stepped profile; basal lobes without webbing fusing inner and outer lobes, outer lobe in lateral view like a very long thin finger, gently curved, nearly equal in length to upper pygofer lobe. Uncal lobes scooplike and gently upturned at their distal ends; lateral processes of uncus in lateral view nearly equal in length to upper pygofer lobes, nearly straight, broadly rounded at apex. Conjunctival claws directed laterally, the distal end of each bearing three sharply-pointed teeth, the central tooth longest. Flabellum absent. Palearis absent.

**Female** (Figs. 61b,d,e). Colour and markings similar to male. Abdominal segment 9 similar in colour to abdomen and thorax; dorsal beak usually darker and sometimes black. Ovipositor sheath dark brown to black and clearly extending beyond dorsal beak.

There are notable differences in size, both within and between populations. Of the limited material available those specimens taken near Cloncurry in January 1984 are largest and very much larger than specimens taken near Georgetown in January 1992. Specimens from Mataranka, Northern Territory, and near Home Hill, northeastern Queensland, are also smallish while those from Adels Grove, northwestern Queensland, are intermediate in size. Size, therefore, shows no geographic trend and is very likely a consequence of availability of nymphal food.

**Distinguishing features.** The uniform body colouration of this species, combined with its lightly tinted wings, makes confusion with any other *Tryella* species unlikely. It is most similar to *occidens*, *noctua* and some individuals of *stalkeri*, but none of these species occurs sympatrically with *crassa*. *Tryella crassa* is immediately distinguished from *occidens*,



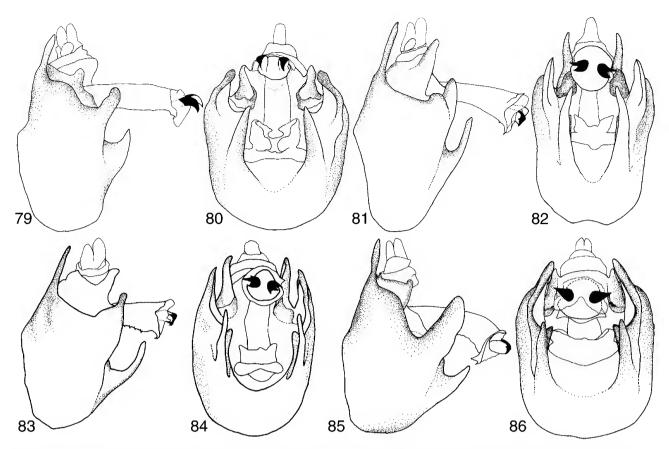
*noctua* and *stalkeri* by the lack of fore wing infuscation anywhere across the base of apical cell 4; the infuscation on *crassa* never passes beyond the base of apical cell 3.

**Distribution** (Fig. 78). Inland regions of monsoonal Northern Territory, where it is known from 80 km SW of Katherine, Mataranka Homestead and the headwaters of the Victoria River, and drier regions of monsoonal Queensland south of the Gulf of Carpentaria to Selwyn mine (160 km SE of Mt Isa) and east almost to Georgetown and far eastern Queensland at Salt Water Creek, 20 km south of Home Hill. Adults emerge after the first heavy summer rains and tend to be very local. There are records from mid December to late February.

Habitat. Adults appear to favour shrubs and low eucalypt saplings where they are usually found on the smaller branches or amongst foliage. However, the populations from 20 km south of Home Hill, Queensland, and from Kalkaringi, NT, were almost exclusively confined to grass in areas where there was a total or substantial absence of trees and shrubs. The species may in fact breed upon grass and males may seek higher advantage points when available from which to call.

**Song.** Singing occurs both during the day and at dusk. Day calling, however, may be restricted to overcast or partly overcast conditions as I have never heard singing on hot sunny days except at dusk. The dusk call is always vigorous. An analysis of the song is under study (Moulds, in prep.).

**Biology**. Mature nymphs are golden brown and glossy except for abdomen below; wing pads light yellowish brown; a dark brown area each side of midline on pronotum; brown patch each side of midline on abdominal segment 8; legs golden brown with fore leg claws dark brown; eyes grey.



Figs. 79–86. Male genitalia of *Tryella* species showing pygofer with uncus and aedeagus in right lateral view (left) and ventral view (right): (79–80) *T. rubra*, genitalia prep. AB53; (81–82) *T. crassa*, genitalia prep. AB9; (83–84) *T. castanea*, genitalia prep. AB15; (85–86) *T. adela*, genitalia prep. AB1.

### Tryella graminea n.sp.

Figs. 24, 57a,b, 87, 92, 93

**Types.** Holotype ♂, K179859, Torrens Creek township, 90 km E of Hughenden, N Queensland, 3.ii.1981, M.S. & B.J. Moulds, AM. Paratypes as follows: NORTHERN TERRITORY—3♂♂ (one genitalic preparation no. AB31), 3♀♀, Ayers Rock, 3.ii.1984, MBM; 1♀, Sixteen Mile Creek, N of Alice Springs, 29.i.1984, MBM; 2♂♂, 2♀♀, Burt Ck, 55 km N of Alice Springs, 24.i.1984, MBM; 5♂♂, 1♀, 5 km S of Taylor Ck, 47 km NE of Barrow Creek township, 23.i.1984, MBM; 1 of, Tennant Creek township, 22.i.1984, MBM; 4 of of, 10 km W of Soudan Hsd, 21.i.1984, MBM; 4♂♂, 25 km NW of Avon Downs Hsd, 21.i.1984, MBM; all in MSM. OUEENSLAND—23 3, K179860 and K179861, 299, K179862 and K179863, Mt Isa, 20.i.1984, MBM; all in AM. 233, 299, Mt Isa, 20.i.1984, MBM; all in BMNH. 333, 19, 85 km SSW of Burketown, 19.xii.1986, MBM; 19, "Gregory Downs", S of Burketown, 6.xii.1982, A. Walford-Huggins; 5 ♂ ♂ (one genitalic preparation no. AB11), Delta Downs Stn., E of Karumba, 16.xii.1987, MBM;  $4\delta\delta$  (one genitalic preparation no. AB106), 399, vicinity Lawn Hill Creek, Lawn Hill NP, 31.x.1996, K.A. Kopestonsky; 8 of of (one genitalic preparation no. AB32), 499, nr Thorntonia Hsd, 120 km ENE of Camooweal, 21.xii.1986, MBM; 233, 80 km NW of Mt Isa, 20.i.1984, MBM; 26 む む (one genitalic preparation no. AB30), 18♀♀, Mt Isa, 20.i.1984, MBM; 54♂♂, 31♀♀, Selwyn mine, 160 km SE of Mt Isa, 1,6,7,16,17,23.ii.1995, 13.iii.1995, T. Woodger; 9♂♂ (one genitalic preparation no. AB33), Malbon, 50 km SSW of Cloncurry, 14.iii.1991, T. Woodger; 1 o, 45 km E of Cloncurry, 5.i.1987, MBM;  $5 \stackrel{?}{\circ} \stackrel{?}{\circ}$ ,  $2 \stackrel{?}{\circ} \stackrel{?}{\circ}$ , 50 km E of Cloncurry, 19.i.1984, MBM;  $1 \stackrel{?}{\circ}$ , 10 km W of Torrens Creek township, E of Hughenden, 7.i.1987, MBM; 49 ♂ ♂ (one genitalic preparation no. AB29), 15 ♀♀, Torrens Creek township, 90 km E of Hughenden, 3.ii.1981, 18.i.1984, MBM; 14♂ ♂, 1♀, Noonbah Hsd, SW of Longreach, 24°07'S 143°11'E, 25,26.i.1998, 4,9.ii.1998, A. Emmott; 12♂♂, 4♀♀, Alpha, 10.ii.1981, MBM; 1♂, Warrego River, 15 km NNE of Charleville, ii.1994, C. Dollery; all in **MSM**. 2♂♂, 2♀♀, Mt Isa, 20.i.1984, MBM; all in **QM**.

**Other material examined.** South Australia—1 &, Oodnadatta [no other data] (SAM).

**Etymology**. From the Latin *graminis* meaning grass and referring to the habitat of the species.

### Description

Male (Figs. 24, 57a, 92, 93). Head. Black; postclypeus ferruginous, often black or tending so around perimeter; anteclypeus black, often with an indistinct light brown patch centrally on midline not visible to naked eye. Rostrum brown basally becoming black apically, reaching bases of hind coxae. Antennae black. Without obvious pubescence above but nearly always bearing considerable silver pubescence below that sometimes extends onto anteclypeus and margins of postclypeus. *Thorax*. Pronotum ochraceous with extreme lateral margin capped brown; a broad ferruginous to black fascia on dorsal midline, this fascia spreading laterally both at its anterior end against pronotal margin as far as eyes, and at its posterior end against pronotal collar; pronotal collar either black or ferruginous or a mixture of both. Mesonotum pale to very dark ferruginous sometimes with a large blackish area anterior of cruciform elevation and a blackish fascia above wing groove; cruciform elevation often tending vellowish brown rather than ferruginous. Thorax above usually lacking pubescence but nearly always covered by silver pubescence below. Wings. Hyaline. Fore wings always with a zigzag

infuscation following basal veins of apical cells 2 and 3 and usually extending to 4; an indistinct infuscation also often present near wing apex at end of vein R1b; venation brown, costa pale muddy yellow or orange brown; basal membrane similar in colour to costa although usually brighter; basal cell faintly tinged amber or sometimes nearly hyaline; costa and veins lacking pubescence visible to naked eye. Hind wing usually with a small infuscation at distal end of vein 2A that sometimes extends part way along its length but some specimens entirely lacking infuscation; venation brown; plaga off-white and usually hidden by a weak amber suffusion on basal half or so of anal lobe. Legs. Medium to light brown; without markings. Opercula. Muddy pale yellow often partly suffused with black; usually covered by fine silver pubescence not obvious to naked eye; clearly separated exposing apex of sternite I and barely concealing tympanal cavities. Abdomen. Tergites brown; some individuals with anterior half of tergite 2 partly or entirely black, dorsal anterior half or more of tergites 3-8 black and 8 also sometimes black along posterior margin. Sternites brown, usually with a diffused dark brown midline. Abdomen above and below without obvious pubescence. Tymbals (Fig. 24). Usually 10 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 92, 93). Pygofer brown; upper pygofer lobes in lateral view broad, upper margin sometimes distinctly curved outwards in central region, distal end upturned with a broad pointed apex, in ventral view angled slightly inwards before midpoint; basal lobes with a broad webbing fusing outer and inner lobes, in lateral view outer lobe just a short fingerlike projection beyond webbing. Uncal lobes scoop-like and gently upturned at their distal ends; lateral processes of uncus in lateral view nearly equal in length to upper pygofer lobes, usually a little constricted near base and angled slightly upwards beyond constriction, apex broadly rounded. Conjunctival claws simple, sharply pointed, directed laterally. Flabellum a large rounded lobe across entire ventral surface. Palearis low and rounded, near distal end of theca.

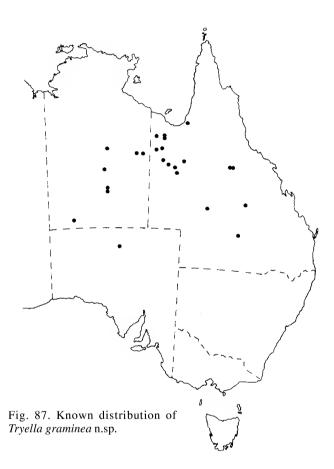
**Female** (Fig. 57b). Colour and markings similar to male. Abdominal segment 9 medium brown, often with dorsal beak dark brown and sometimes with dark brown patches mainly dorsally. Ovipositor sheath black and clearly extending beyond dorsal beak.

**Measurements.** n = 10 ♂ ♂, 10 ♀ ♀ (includes smallest and largest of available specimens). *Length of body*: male 15.5–19.0 (17.1); female 15.7–18.4 (17.5). *Length of fore wing*: male 19.1–21.9 (20.3); female 19.4–23.1 (21.1). *Width of head*: male 5.2–5.7 (5.4); female 5.2–5.7 (5.5). *Width of pronotum*: male 5.8–6.5 (6.2); female 5.8–6.9 (6.4).

**Distinguishing features**. A reasonably distinctive species that always has an obvious zigzag infuscation on the fore wing, a pale pronotum that contrasts markedly with a much darker mesonotum and darkened pronotal midline. The fore wings are broader and shorter than most other *Tryella* species with a fore wing length to hind wing length ratio clearly less than 2:1 (approximately 1.7:1).

Within the geographic range of graminea the most similar species are T. ochra and T. castanea and some individuals of T. willsi. Both ochra and castanea rarely have bold zigzag infuscations on the fore wings and, unlike graminea, ochra has a fore wing/hind wing length ratio approaching 2:1 and castanea entirely lacks amber suffusion on the hind wing anal lobe. Those individuals of T. willsi with dark reddish brown on the thorax above instead of the usual black, differ from graminea in having a fore wing/hind wing ration at least 1.8:1.

*Tryella graminea* is the only *Tryella* species with distinct colour morphs (fore wing costa and fore wing basal membrane either orange or pale yellow).



**Distribution** (Fig. 87). Central Australia south from Tennant Creek in Northern Territory to Oodnadatta in South Australia and west to Ayers Rock, and north-west and central Queensland from the Gulf of Carpentaria to Charleville. Adults emerge after heavy summer rains and are often locally common. There are records from late October to mid March.

**Habitat**. Native and introduced grasses, where adults tend to form local populations. Long, partly dead grass appears to be favoured.

# Tryella infuscata n.sp.

Figs. 65a,b, 71, 72, 88

**Types.** QUEENSLAND—Holotype  $\delta$ , K179856, 120 km S of Normanton, 14.i.1986, M.S. & B.J. Moulds, in AM. Paratypes as follows:  $3\delta\delta$  (2 male genitalic preparations Nos AB79, AB86), 7 same data as holotype; all in MSM.

**Other material examined** Northern Territory—1 &, Alexandria [19°03'S 136°42'E], S Australia, G.N. Stalker, 1907-261 (a paralectotype of *T. stalkeri*); all in **BMNH**. This specimen is labelled as coming from "S. Australia" because the Northern Territory was at that time administered by South Australia.

**Etymology**. From the Latin *infuscatus* and referring to the bold infuscations on the fore wings of this species.

#### **Description**

Male (Figs. 65a, 71, 72). Head. Ferruginous with areas of black concentrated around ocelli, around eyes except on supra-antennal plates and below; postclypeus and anteclypeus ferruginous. Rostrum ferruginous becoming black to varying extent towards apex but usually with extreme apex brown; passing bases but not reaching apices of hind coxae. Antennae brown to nearly black. Usually bearing some silver pubescence, especially below. *Thorax*. Pronotum ochraceous with a broad middorsal fascia dark ferruginous, this fascia spreading laterally both at its anterior end against pronotal margin to about eyes, and at its posterior end against pronotal collar; pronotal collar dark ferruginous often tending black, especially at lateral angles. Mesonotum dark ferruginous, usually with a dorsal pair of ill-defined obconical markings based on anterior margin weakly outlined in yellowish brown; cruciform elevation yellowish brown. Thorax above usually lacking noticeable pubescence; below medium to light brown and always with distinct silver pubescence. Wings. Hyaline. Fore wings always with a zigzag infuscation following basal veins of apical cells 2-4 and usually along the length of vein R1b forming base of apical cell 1, and to a lesser degree at distal end of apical cell 1; venation brown, costa muddy pale yellow; basal cell barely tinted brown; basal membrane orange, sometimes tending yellowish. Hind wings with an infuscation at distal extremity of vein 2A against wing margin; plaga off white; anal lobe weakly tinted brown primarily on basal two thirds; venation light brown to pale yellow. Legs. Brown without obvious markings. Opercula. Yellowish brown; almost meeting and barely concealing tympanal cavities; usually covered by silver pubescence not always obvious to naked eye. Abdomen. Tergites dark ferruginous with mid brown posterior margin and ventral surface mid brown; tergite 2 usually dominantly mid brown laterally and tergite 8 usually entirely mid brown except for dorsal anterior half. Sternites brown. Abdomen above and below often with silver pubescence not always visible to naked eye. Tymbals. Usually 10–11 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 71, 72). Pygofer dark ferruginous dorsally and on upper pygofer lobes, otherwise mid brown; upper pygofer lobe in lateral view very broad at base, gradually tapering to a blunt point, usually with a slight upward curve, in ventral view gently curving inwards; basal lobe in lateral view like a very long thin finger, gently curved, nearly equal in length to upper pygofer lobe, not fused with inner secondary lobe by broad webbing. Uncal lobes scoop-like and gently upturned at

their distal ends; lateral process of uncus in lateral view small and rounded. Conjunctival claws simple, sharply pointed, directed ventrally. Palearis narrow; along much of length of theca and reaching distal end, gradually tapering to zero at proximal end.

**Female** (Fig. 65b). Colour and markings similar to male. Abdominal segment 9 brown, sometimes with dorsal beak dark ferruginous. Ovipositor sheath nearly black with brown ventral surface; extending just beyond dorsal beak.

**Distinguishing features.** Distinguished from other species with extensive fore wing infuscations that reach to top of ulnar cell 3 (i.e. *noctua*, *occidens* and *stalkeri*) by its dark mesonotum and pale pronotum which bears a broad dark midline. Occasional individuals of *T. stalkeri* possess similar colouring; these can be separated (apart from distribution) by the anal lobe which is suffused golden amber in *stalkeri* and brown in *infuscata*. Male genitalia clearly differ in the size of the uncal lateral process which, in lateral view, is large and tapering in *stalkeri* (Fig. 67) but small and rounded in *infuscata* (Fig. 71).

**Distribution** (Fig. 88). Known only from inland districts below the Gulf of Carpentaria. There are just two known localities: 120 km south of Normanton in Queensland and Alexandria Station in Northern Territory.

**Habitat**. Adults most likely inhabit eucalypt trees. All known specimens have been taken at light.

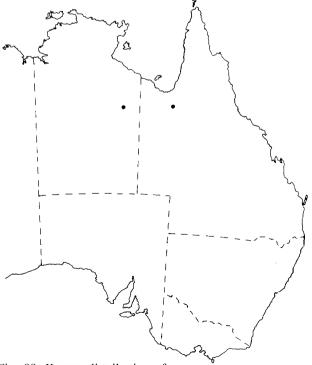


Fig. 88. Known distribution of *Tryella infuscata* n.sp.

#### Tryella kauma n.sp.

Figs. 11, 25, 52a,b, 89, 96, 97

**Types.** Queensland—Holotype &, K179842, Walkers Ck, 35 km NNE of Normanton, 16.xii.1986, M.S. & B.J. Moulds, in AM. Paratypes as follows:  $1 \, \mathring{\circ}$ ,  $1 \, \mathring{\circ}$ , same data as holotype;  $1 \, \mathring{\circ}$ ,  $1 \, \mathring{\circ}$ , 50 km SE of Normanton, 15.i.1986, MBM; all in AM.  $1 \, \mathring{\circ}$ , Wernadinga Stn, SE of Burketown, 18.xii.1986, MBM;  $18 \, \mathring{\circ} \, \mathring{\circ} \, ($  one male genitalic preparation no. AB12),  $14 \, \mathring{\circ} \, \mathring{\circ} \,$ , same data as holotype;  $2 \, \mathring{\circ} \, \mathring{\circ} \, \mathring{\circ} \,$ , same data as holotype but 2.i.1990, 15.i.1992;  $25 \, \mathring{\circ} \, \mathring{\circ} \, ($  one male genitalic preparation no. AB78),  $18 \, \mathring{\circ} \, \mathring{\circ} \, ,$  50 km SE of Normanton, 15.i.1986, MBM;  $15 \, \mathring{\circ} \, \mathring{\circ} \, \mathring{\circ} \, ($  one male genitalic preparation no. AB3),  $18 \, \mathring{\circ} \, \mathring{\circ} \, \mathring{\circ} \, ($  sast Haydon, 60 km SE of Normanton, 15.i.1986, MBM;  $1 \, \mathring{\circ} \, , 25 \, \mathring{\circ} \, ($  sast Haydon, 60 km SE of Normanton, 15.i.1986, MBM;  $1 \, \mathring{\circ} \, , 25 \, \mathring{\circ} \, ($  sast Haydon, 60 km SE of Normanton, 15.i.1986, MBM, all in MSM.  $1 \, \mathring{\circ} \, , 1 \, \mathring{\circ} \, , 1 \, \mathring{\circ} \, ($  sast Haydon, 60 km SE of Normanton, 15.i.1986, MBM, both in QM.

**Etymology**. From the Greek *kauma* meaning burning heat and referring to the hot climatic conditions prevailing in the area where the species is found.

#### Description

Male (Figs. 25, 52a, 96, 97). Head. Black but usually with variable amounts of brown visible under magnification. nearly always partly or entirely brown on antennal plates and often to some extent between eyes and ocelli; postclypeus and anteclypeus ferruginous. Rostrum muddy pale yellow basally, darkening on labium and becoming black towards apex but always with extreme apex dark brown; passing beyond bases of hind coxae but never reaching their apices. Antennae black or brown but usually with basal segment, and sometimes part of second segment, brown. Without extensive silver pubescence above but usually extensive below except of clypeus. Thorax. Pronotum ochraceous with a broad middorsal fascia pale to very dark ferruginous or sometimes nearly black, this fascia spreading laterally both at its anterior end against pronotal margin to about eyes and at its posterior end against pronotal collar; pronotal collar ferruginous to nearly black but always pale anterior of lateral angles. Mesonotum ferruginous, often black or very dark brown immediately anterior of cruciform elevation and along lateral margin above wing bases; cruciform elevation usually light brown but sometimes dark. Thorax above often lacking noticeable pubescence; below medium to light brown and always with distinct fine silver pubescence. Wings. Hyaline. Fore wings usually with some infuscation limited to bases of apical cells 1-3 and apex of apical cell 1, sometimes continuous but often broken and occasionally entirely without infuscation; venation brown, costa pale to medium ochraceous but sometimes tinted ferruginous; basal cell hyaline; basal membrane orange or orange yellow. Hind wings with a weak infuscation at the distal end of vein 2A and often following along much of the length of 2A, sometimes also adjacent to off white plaga on 3A; venation brown. Legs. Light to medium brown; without markings. Opercula. Muddy yellow, usually with very narrow black edge along lateral margin; usually covered by silver pubescence not always obvious to naked eye; clearly separated exposing apex of sternite I and barely concealing tympanal cavities. Abdomen. Tergites brownish orange to dark brown, often with tergite 1 black or nearly so, often tergites 2 and 3 partly or entirely black on anterior half and sometimes also on tergites 4–7; tergite 8 usually black or dark brown on anterior half. Sternites light brown. Abdomen above and below often



with silver pubescence not always visible to naked eye. Tymbals (Fig. 25). Usually 9 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 96, 97). Pygofer brownish orange to dark brown; upper pygofer lobes in lateral view broad, upper margin distinctly curved outwards in central region, lower margin curved upwards near distal end towards an upturned pointed apex, in ventral view angled slightly inwards; basal lobes with a broad webbing fusing outer and inner lobes, in lateral view outer lobe just a short finger-like projection beyond webbing. Uncal lobes scoop-like and gently upturned at their distal ends; lateral processes of uncus in lateral view nearly equal in length to upper pygofer lobes, angled slightly upwards from near base, apex tapering to a rounded point. Conjunctival claws simple, sharply pointed, directed laterally. Flabellum a large rounded lobe across entire ventral surface. Palearis absent.

**Female** (Figs. 11, 52b). Colour and marking similar to male. Abdominal segment 9 brown, tending palest ventrally; dorsal beak dark brown or black. Ovipositor sheath black and clearly extending beyond dorsal beak.

**Measurements.** n =  $10 \ \delta \ \delta$ ,  $10 \ \$  (includes smallest and largest of available specimens). *Length of body*: male 11.6–15.8 (13.8); female 13.8–17.1 (15.8). *Length of fore wing*: male 15.3–20.7 (18.3); female 17.7–20.6 (19.8). *Width of head*: male 4.6–5.9 (5.1); female 4.9–6.0 (5.4). *Width of pronotum*: male 4.7–6.0 (5.1); female 4.8–6.1 (5.5).

**Distinguishing features.** Although *T. kauma* is confined to Queensland, adults closely resemble *T. adela* from the Northern Territory and the form of *T. castanea* found near the Victoria River, Northern Territory. There are, however,

clear differences between these species in male genitalia (compare Figs. 84, 86 and 97). Electrophoretic comparison between *castanea* and *kauma* (Serkowski & Moulds, unpub. data) showed a 21% fixed difference, clearly separating these two species; electrophoretic data comparing *kauma* and *adela* were not available.

Within the range of *T. kauma* there can be close resemblance with some individuals of *T. ochra* and *T. burnsi* although the latter species may not be sympatric as there is doubt about the identity of the single record falling within the range of *kauma*. Usually *kauma* can be distinguished from *ochra* and *burnsi* by its smaller size (fore wing length never reaching 22 mm) and by having the fore wing basal cell hyaline. The known distribution of *T. castanea* approaches close to that of *kauma* and may be sympatric around Burketown or Normanton. *Tryella kauma* can be distinguished from *castanea* using the same characters that distinguish *kauma* from *burnsi*.

**Distribution** (Fig. 89). Lower Gulf region of Queensland east to near Georgetown. There are records from only Wernadinga Station SE of Burketown, near Normanton, near Croydon and 25 km W of Georgetown. Adults have been taken from mid December to mid January, after heavy summer rains.

**Habitat.** Adults most likely inhabit eucalypt trees and saplings. Nearly all known specimens have been taken at light. The single specimen from Wernadinga Station was taken in grass but this was most likely an accidental occurrence.

**Song.** Singing occurs both during the day and especially at dusk.

# Tryella lachlani n.sp.

Figs. 12, 56a,b, 73, 74, 90

Species "G" Ewart, 1993: 139–140, fig. 14. *Abricta* sp.–Zborowski & Storey, 1995: 87 (figured).

**Etymology**. Named after Robert Lachlan who collected the first examples of this species seen by me, as well as many other rare and valuable cicadas.

#### **Description**

Male (Figs. 56a, 73, 74). *Head.* Black with ferruginous postclypeus that sometimes has its midline blackened; anteclypeus ferruginous to black. Rostrum brown and black, usually black dorsally and at apex; passing bases

but not apices of hind coxae. Antennae black or brown. Head usually with some fine silver pubescence, primarily confined to lorum below. *Thorax*. Pronotum ochraceous with a broad black middorsal fascia that spreads laterally both against anterior margin to back of eyes and against posterior margin to merge with black pronotal collar. Mesonotum ferruginous except for black around cruciform elevation, this black pale on teneral or partly teneral individuals. Thorax above usually without obvious silver pubescence. Thorax below black or nearly so and bearing fine silver pubescence. Wings. Hyaline. Fore wings usually without noticeable infuscations but often with an extremely weak infuscation at distal end of apical cell 1 and a few individuals also very weakly infuscated at base of apical cell 2 and sometimes 3; venation black or sometimes brown, costa ochraceous; basal cell weakly tinted translucent amber; basal membrane orange; costa and veins on basal third or so sometimes bearing a little silver pubescence not visible to naked eye. Hind wings with a smoky black infuscation at distal end of vein 2A which, in most specimens, fills the distal end of anal lobe, the proximal end sharply pointed; remainder of anal lobe suffused translucent amber hiding cream plaga; venation tending pale brown basally becoming dark towards apex. Legs. Ferruginous often with black in region of fore leg femoral spines. Opercula. Black or nearly so; usually covered by silver pubescence not always obvious to naked eye; clearly separated exposing apex of sternite I and barely concealing tympanal cavities. Abdomen. Tergites black with much of dorsal and subdorsal area ochraceous; tergite 2 substantially black; tergite 3 black with ochraceous dorsal band along posterior margin; tergites 4-7 dominantly ochraceous with black increasingly reduced to sublateral region; tergite 8 black on anterior half or a little less, otherwise ferruginous. Sternite 2 black; sternites 3–8 ferruginous, 3–6 often with pale cream posterior margins to varying extent. Abdomen above and below without noticeable pubescence. Tymbals. Usually 11 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 73, 74). Pygofer black and ochraceous, usually black dorsally and partly or entirely so laterally; upper pygofer lobe in lateral view very broad at base, gradually tapering to a sharp or rounded point at apex, and usually very gently curved upwards, in ventral view nearly straight and tilted slightly inwards; basal lobe in lateral view like a very long thin finger, gently curved, nearly equal in length to upper pygofer lobe, not fused with inner secondary lobe by broad webbing. Uncal lobes scoop-like and gently upturned at their distal ends; lateral process of uncus in lateral view small and rounded. Conjunctival claws simple, sharply pointed, directed ventrally. Flabellum a very small mid-ventral rounded lobe. Palearis adjoining flabellum and continuing along much of length of theca, small and gradually tapering to zero at proximal end.

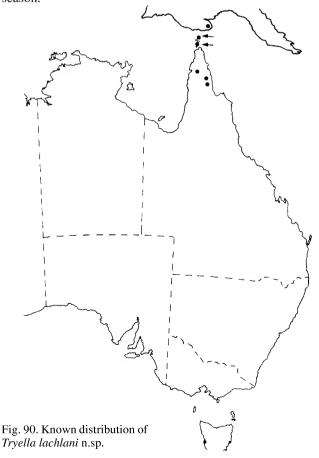
Female (Figs. 12, 56b). Colour and markings similar to male except for abdomen above. Dorsal and subdorsal areas dominantly ochraceous but usually less brilliant than that of male, otherwise black; a black middorsal blotch usually present at base; tergite 8 always with a distinct black band following anterior margin. Abdominal segment 9 dull ochraceous to brown with dorsal area and dorsal beak black. Ovipositor sheath black or dark brown; extending clearly beyond dorsal beak.

**Measurements.** n = 10 ♂ ♂, 10 ♀ ♀ (includes smallest and largest of available specimens). *Length of body*: male 15.1–19.2 (17.0); female 17.1–20.0 (18.4). *Length of fore wing*: male 22.1–25.3 (23.1); female 22.0–27.1 (24.1). *Width of head*: male 5.7–7.1 (6.3); female 6.4–7.0 (6.8). *Width of pronotum*: male 5.7–7.3 (6.4); female 6.2–7.2 (6.9).

**Distinguishing features**. It is unlikely that the distinctive male of this species, with its bright ochraceous pronotum and abdominal tergites, will be confused with that of any other *Tryella* species.

Females are less distinctive but nevertheless are readily identifiable by their ochraceous pronotum and abdomen, lack of (or rudimentary) fore wing infuscations and their black or blackish cruciform elevations. Confusion is most likely to occur between atypical females of *lachlani* and atypical females of *burnsi*; the black cruciform elevation of *lachlani* immediately distinguishes it from *burnsi* which always has the cruciform elevation light brown. The *Key to species* should resolve doubtful cases.

**Distribution** (Fig. 90). South-west Papua New Guinea, Torres Strait islands and northern Cape York Peninsula of Queensland. The specimen from Oriomo on mainland Papua New Guinea just north of Daru Island, represents the only record of any *Tryella* or allied species from Papua New Guinea. From Queensland there are records from just five localities, Moa Island (= Banks Is.), Hammond Island, near Heathlands Station (Ewart, 1993), York Downs (50 km east of Weipa) and near Mt Croll (near Coen). This species is sometimes locally common. Adults have been taken in December and January but they may also occur later in the season.



**Habitat.** Open *Melaleuca* woodland where adults favour the outer branches of these trees. There are no confirmed reports of adults inhabiting other tree species.

**Song.** Adults sing both during the day and at dusk. Ewart (1993) describes the song of this species (his Species G) as "a continuous, rapidly pulsating, high pitched humming, quite soft, and not easily located". A frequency range from 1–10kHz was noted by Ewart and he provides an oscillogram and frequency graph of the call.

# Tryella noctua (Distant, 1913), n.comb.

Figs. 26, 48, 49, 64a,b, 91

Abricta noctua Distant, 1913: 487; Ashton, 1915: 91; Distant, 1915: 53; Burns, 1957: 636, 637; Metcalf, 1963: 209; Duffels & van der Laan, 1985: 235; Moulds, 1990: 121–122, pl. 15, figs 2, 2a.

Abricta rufonigra Ashton, 1914: 349, pl. 17.

#### **Types**

(a) Abricta noctua. Lectotype male here designated, bearing four labels: (i) "Abricta/noctua/Dist./type" handwritten in black ink, probably original Distant label; (ii) "Type/H.T." small white circular label with red border on which is machine printed; (iii) "SYN-/TYPE" small white circular label with blue border on which is machine printed; (iv) "Australia./W.W.Froggatt,/1913-364" rectangular machine printed label (in BMNH). Examined.

Lectotype designation. Distant (1913) did not designate a holotype or state the number of specimens examined. While it is probable that he had only the one specimen listed above, following Recommendation 73F of the Code to consider such specimens as syntypes, and in the absence of any other previous designation of this specimen as type, this specimen is designated lectotype.

Type locality. The last label listed above for the lectotype is a BMNH label indicating from where the Museum obtained the specimen and its registration number. There is no label giving locality, date of collection or name of collector. The original description states "Hab. N.W. Australia, Cue (H.W. Brown, type in Brit. Mus.)" and there is no reason to doubt that this is the true type locality.

(b) Abricta rufonigra. Lectotype male here designated (in SAM) (examined). Bearing three labels as follows: (i) "Cue, W.A./H.W. Brown" small machine printed label; (ii) "Abricta rufonigra Ashton./Type" hand printed in India ink; (iii) "Abricta rufonigra Ashton./Syn. of A. noctua Dist./W.A./Type. I2939, I4960".

Lectotype designation. Ashton's (1914) description of A. rufonigra is based on an unstated number of specimens of unstated sex from "Western Australia: Cue", although it is likely that only one male was available for the description. In the SAM there are a further male and two females bearing similar data as the specimen labelled "Type". However, measurements of one of the females are not compatible with those stated in the original description despite an additional label attached to this specimen stating "2939 Abricta rufonigra" and what appears to be the words "willsi W L Dist" and "n. sp.". Further, there are two males and two females in ANIC also labelled Cue and possibly old enough to have been seen by Ashton.

While it is most likely that the male "type" is in fact a holotype it is not possible to categorically deny it forms part of a syntype series. To clarify the identity of this name the specimen detailed above is here designated lectotype.

**Note on synonymy.** Following publication of his description of *A. rufonigra*, Ashton found that Distant had described the species as *A. noctua* the preceding year. Consequently Ashton (1915) placed *A. rufonigra* as a junior synonym of *A. noctua*. H.W. Brown often divided his field catches between Distant and Ashton which also led to the creation of synonymies for other cicada species.

Material examined. Types and the following: WESTERN AUSTRALIA—13, K179960, 19, K179961, Cue, no date, H.W. Brown, H. Ashton Coll.; 19, K179836, 55 km SE of Leinster, 28°20'S 121°05'E, 16.i.1989, MBM; 1♂, K179835, Leonora, 15.i.1989, MBM; all in AM. 233, 299, Cue, ex W.W. Froggatt Collection; all in ANIC. 13, 60 km W of Sandstone, 18.i.1989, MBM; 1♂, 1♀, Sandstone, 18.i.1989, MBM; 19, 40 km E of Sandstone, 17.i.1989, MBM; 13, "Depot Springs", 27°56'S 120°05'E, 17.i.1989, MBM; 1♂, 3♀♀, Agnew, 17.i.1989, MBM; 1♂, 4♀♀, 17 km ENE of Agnew, 27°59'S 120°41'E, 17.i.1989, MBM; 7♂♂, 11♀♀, 55 km SE of Leinster, 28°20'S 121°05'E, 16.i.1989, MBM; 9♂♂ (1 male genitalic preparation no. AB22), 11♀♀ (1 \, ex exuviae), Leonora, 15,16.i.1989, MBM; 1 \, White Cliffs [NE of Laverton], 18.i.1978, M. Powell; all in MSM. 13, 299, Cue, (no date), H.W. Brown; all in SAM. 19, 55 km SE of Leinster, 28°20'S 121°05'E, 16.i.1989, MBM; 1&, Leonora, 15,16.i.1989, MBM; 1&, reg. no. 34332, Winburn Rocks, 94 km E of Warburton, 26°05'S 127°30′E, 22.i.1990, T.F. Houston & M.S. Harvey; 3♂♂, 1♀, reg. nos. 34326-34329, 2.5 km N of Mt Linden, 29.19'S 122.25'E, 17-23.iii.1979, T.F. Houston *et al.*; 1♀, reg. no. 34317, Weld Range, 2.iii.1963, A. Douglas; 19, reg. no. 34318, Prairie Downs Stn, i/iii.1963, C. Snell; 19, reg. no. 34320, Mileura, nth Cue, 16.xii.1969, E. Lindgreen; 19, reg. no. 34319, 50 m W Charles Knob, approx. 300 m NE Laverton, 25°S 124°E, 30.i.1964, M. Gillett; 3♂♂, 3♀♀, reg. nos 34302, 34321, 34323-34325, 34333, 3.8 km, c. 7 km NE and 13.8 km ENE of Comet Vale Siding, 29°57'S 121°07'E, 7-15.iii.1979, T.F. Houston et al.; 299, reg. nos. 34330-34331, 6 km NE of Mt Cooper, 26°11'S 127°57'E, 21.i.1990, T.F. Houston & M.S. Harvey; 19, reg. no. 34322, same data but, on branches of mulga; all in WAM. NORTHERN TERRITORY—3♂♂, 1♀, small hill 20 km E of Glen Helen Gorge, 28.i.1984, MBM; 3♂♂, Ayers Rock, 3.ii.1984, MBM; all in MSM. South Australia—855, 399, 17 km S of Chandler railway siding, 5.ii.1984, MBM; 1♂, 2♀♀, 24 km NW of Marla, 5.ii.1984, MBM; 13, 19, 30 km S of Mt Willoughby Stn, 6.ii.1984, MBM; 13, 13 km N of The Twins Hsd, Stuart Hwy, 7.ii.1984, MBM; 2♂♂, 1♀, Coober Pedy, 23.xii.1988, S. Lamond; all in MSM.

# Description

Male (Figs. 26, 48, 49, 64a). Head. Black, often with a very small muddy yellow marking on midline against posterior margin not discernible to naked eye; postclypeus black, sometimes with areas dark ferruginous, below often with a yellow margin barely discernible to naked eye; anteclypeus black, sometimes with a little ferruginous not discernible to naked eye. Rostrum tending brown basally but otherwise black; reaching bases of hind coxae. Antennae black. Often bearing some silver pubescence, especially below. Thorax. Pronotum with a broad black fascia on dorsal midline, otherwise dark ferruginous; pronotal collar black, on some individuals tending partially brown on lateral angles. Mesonotum sometimes almost entirely black but usually dark ferruginous with black markings, the black appearing as a fascia bordering wing grooves and as a broad middorsal fascia that often incorporates a pair of very dark ferruginous obconical markings based on anterior margin; cruciform elevation black or dark brown. Thorax above often with some silver pubescence; below usually substantially covered by silver pubescence. Wings. Hyaline. Fore wings

always with a bold zigzag infuscation following basal veins of apical cells 2-4 and usually also along the length of vein R1b forming apical cell 1; venation black, costa dark brown; basal cell barely tinted brown; basal membrane dark grey; costa and veins on basal half or so of wing usually with some silver pubescence not always discernible by naked eye. Hind wings with infuscations bordering plaga along vein 2A and 3A; plaga off white; venation muddyyellow to brown. Legs. Black and brown to varying extent but usually with tibiae dominantly black. Opercula. Brown to nearly black but usually tending brown across posterior margin; often bearing fine silver pubescence usually discernible to naked eye; clearly separated exposing apex of sternite I and barely concealing tympanal cavities. Abdomen. Tergites black or nearly so, sometimes with a little dark brown mainly confined to tergites 2 and 8. Sternites dark brown with a broad black midline, sometimes almost entirely black, the black always reaching full width of sternite VII but contracting on its anterior half; sternite VIII always entirely black or nearly black. Abdomen above and below usually with silver pubescence visible to naked eye. Tymbals (Fig. 26). Usually 10 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 48, 49). Pygofer black or nearly so; upper pygofer lobes in lateral view broad, slightly tapering to a broad rounded apex, in ventral view slightly angled inwards with the subdivision of terminal section clearly visible externally as a stepped profile; basal lobes without webbing fusing inner and outer lobes, outer lobe in lateral view like a very long thin finger, gently curved, almost equal in length to upper pygofer lobe. Uncal lobes scoop-like and gently upturned at their distal ends; lateral processes of uncus in lateral view broad at base but steeply tapering on basal third, thereafter narrow and parallel-sided, apex rounded. Conjunctival claws simple, sharply pointed, directed ventrally. Flabellum absent. Palearis on distal third of theca, reaching distal end, nearly even in width but tapering abruptly at proximal end.

**Female** (Fig. 64b). Colour and markings similar to male. Abdominal segment 9 black dorsally, usually becoming partially dark brown ventrally. Ovipositor sheath black; clearly extending beyond dorsal beak.

**Measurements.** n = 10 ♂ ♂, 10 ♀ ♀ (includes smallest and largest of available specimens). *Length of body*: male 18.6–24.4 (22.0); female 20.3–25.8 (23.7). *Length of fore wing*: male 23.8–29.0 (26.9); female 25.7–31.9 (29.0). *Width of head*: male 6.6–8.0 (7.4); female 6.9–8.6 (7.8). *Width of pronotum*: male 6.8–8.9 (7.9); female 7.4–9.4 (8.5).

**Distinguishing features**. This species is remarkably similar to *T. occidens* but is easily distinguished by the colour of the postelypeus which is black or very nearly so in *noctua* but ferruginous brown in *occidens*. However, there are major differences in male genitalia between these two species (see *T. occidens* for details).

There is also similarity between *T. noctua* and darker individuals of *T. stalkeri*. The latter species is never nearly black and the hind wing plagal area along vein 3A entirely devoid of black.

**Distribution** (Fig. 91). Arid regions of Central and Western Australia south of the Tropic of Capricorn in areas receiving less than 300 mm average annual rainfall. From Western

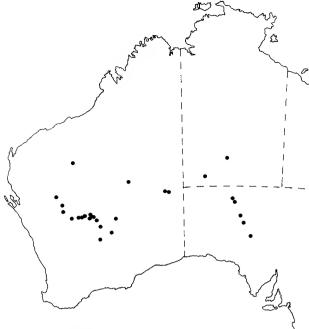


Fig. 91. Known distribution of Tryella noctua (Distant).

Australia there are records from as far west as Mileura Station, north as far as Prairie Downs and south to Comet Vale near Menzies. From the Northern Territory there are records from a small hill 20 km east of Glen Helen Gorge, and from near Ayers Rock. All South Australian records are from along the Stuart Hwy between Chandler and Coober Pedy. Adults have been taken from mid December to late March.

**Habitat**. Mulga (*Acacia aneura*) and possibly other shrubs and small trees. Adults tend to perch along small branches where they are often well camouflaged.

**Song.** Adults sing both during the day and at dusk; otherwise unknown.

# Tryella occidens n.sp.

Figs. 66a,b, 100-102

**Types.** Western Australia—Holotype  $\eth$  (genitalic preparation no. AB23), K179834, Carnarvon, 26.ii.1977, MBM, in **AM**. Paratypes as follows:  $4\eth \eth$ ,  $2 \heartsuit \diamondsuit$ , Carnarvon, 24,25,26.ii.1977, MBM;  $2\eth \eth$  (one male genitalic preparation no. AB24), Carnarvon, 4.ii.1975, 10.v.1981, K. & E. Carnaby;  $1\eth$  (genitalic preparation no. AB48),  $4\heartsuit \diamondsuit$ , Lyndon R. crossing, NW Coastal Hwy, 28.ii.19184, 19.ii.1985, at light, K. & E. Carnaby; all in **MSM**.  $1\eth$ , Gascoyne R, Carnarvon, 3.iii.2001, P. Hutchinson, in **PH**.

**Etymology**. From the Latin *occidens* meaning in the direction of the setting sun and referring to the extreme western distribution of this species in Australia.

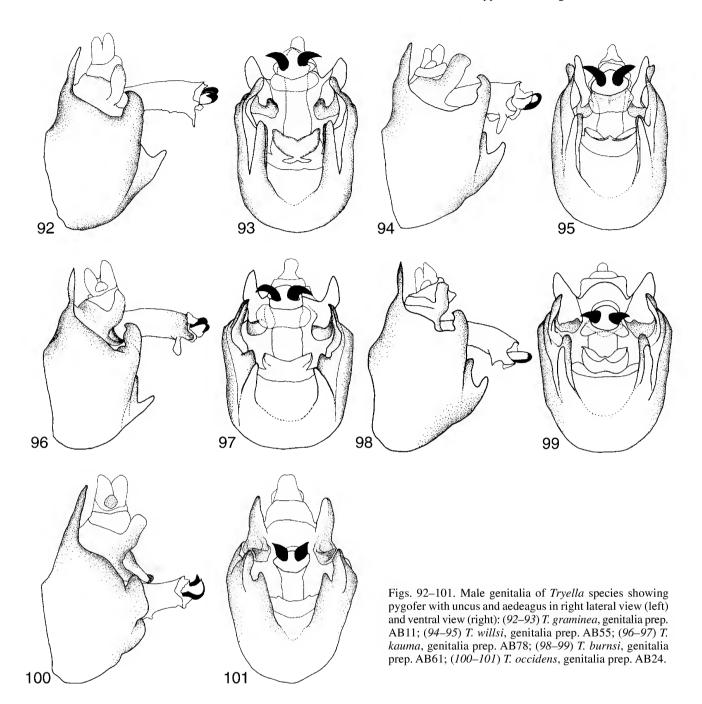
#### Description

Male (Figs. 66a, 100, 101). *Head*. Black or dominantly so on most individuals, sometimes dark ferruginous, and usually with a very small muddy yellow marking on midline against posterior margin, not discernible to naked eye; postclypeus ferruginous; anteclypeus ferruginous but

usually a little darker than postclypeus except along midline. Rostrum muddy yellow basally becoming black towards apex particularly on labium, but always with extreme apex dark brown; reaching to or just beyond bases of hind coxae. Antennae black or sometimes dark brown. Often bearing some silver pubescence, especially below. Thorax. Pronotum dark ferruginous, sometimes with a broad fascia along midline a little darker or a little paler than remainder; pronotal collar usually very dark ferruginous, especially at lateral angles. Mesonotum dark ferruginous, sometimes with an adjacent pair of obconical markings based on anterior margin a little paler; cruciform elevation similar in colour to majority of mesonotum. Thorax above often with some silver pubescence; below substantially covered by silver pubescence. Wings. Hyaline. Fore wings always with a bold zigzag infuscation following basal veins of apical cells 2-4 and also along the length of vein R1b forming apical cell 1; venation and costa brown; basal cell tinted brown, sometimes barely so; basal membrane dark grey to brown; costa and veins on basal half or so of wing usually with some silver pubescence, not always discernible to naked eye. Hind wings with infuscations bordering plaga along veins 2A and 3A; plaga off white, following length of vein 2A, almost the length of 3A, and the inner margin of anal lobe almost to distal end of 3A; venation muddy yellow, sometimes tending brown. Legs. Mid brown, without obvious tonal contrasts or markings. *Opercula*. Medium to dark grey tending yellowing or reddish brown and with little tonal variation; often bearing fine silver pubescence usually visible to naked eye; clearly separated, exposing apex of sternite I and barely concealing tympanal cavities. Abdomen. Dark ferruginous to nearly black, of even or nearly even tone but usually with tergite 2 paler laterally and tergite 8 black or nearly so along posterior margin. Sternites similar in colour to tergites although sometimes a little paler near base. Abdomen above and below usually with silver pubescence visible to naked eye. Tymbals. Usually 11 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 100, 101). Pygofer dark ferruginous to nearly black; upper pygofer lobes in lateral view stunted, very broad and rounded, in ventral view tilted slightly inwards; basal lobe entirely lacking outer lobe, the inner lobe normal. Uncal lobes with mediodistal part of each developed into a robust hook turned outwards and upwards; lateral processes of uncus in lateral view well-developed, straight, parallel-sided, apex nearly square. Conjunctival claws simple, sharply pointed, directed dorsolaterally. Flabellum absent. Palearis a small rounded flange set on a small but prominent raised lobe situated about one quarter length of theca from its distal end.

**Female** (Fig. 66b). Colour and markings similar to male. Abdominal segment 9 usually slightly paler than tergites; dorsal beak usually darker and sometimes nearly black. Ovipositor sheath ferruginous brown usually darkest towards apex; clearly extending beyond dorsal beak.

**Measurements.** n = 8 ♂ 3 and 6 ♀ ♀ (includes all available specimens). *Length of body*: male 19.5–22.0 (20.6); female 21.0–24.0 (23.4). *Length of fore wing*: male 24.9–27.7 (26.5); female 25.8–29.5 (28.2). *Width of head*: male 7.3–7.8 (7.5); female 7.3–8.6 (8.0). *Width of pronotum*: male 7.4–9.0 (8.0); female 7.9–9.1 (8.6).



**Distinguishing features**. This species is remarkably similar to *T. noctua* but can be distinguished by the colour of the postclypeus which is ferruginous in *occidens* but black or nearly so in *noctua*. However, there are major differences in male genitalia between these two species, the most significant being the direction of the conjunctival claws (outturned and partly upturned in *occidens*, downturned in *noctua*) and the shape and position of the lateral processes of the uncus and the basal pygofer lobes (broad and adjacent in *occidens*, relatively slender and widely separated on *noctua*—compare Figs. 48 and 100).

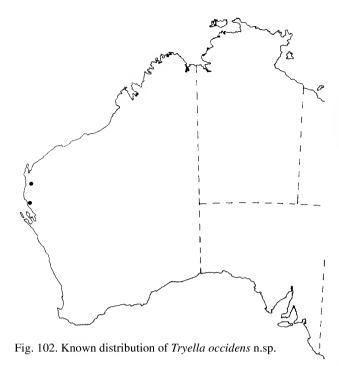
The male genitalia of *occidens* clearly differ from all other *Tryella* species. The partially upturned conjunctival

claws are unique and the upper pygofer lobes are short and rounded with a low profile.

*Tryella occidens* is also similar to darker individuals of *T. stalkeri*. The latter species lacks the black pigmentation on the hind wing adjacent to vein 3A that is always obvious on *occidens*.

**Distribution** (Fig. 102). Far west of Western Australia where there are records only from around Carnarvon and the Lyndon River crossing some 150 km north of Carnarvon. Adults have been taken in February, March and May.

Habitat. Adults inhabit trees or large shrubs.



#### Tryella ochra n.sp.

Figs. 27, 55a,b, 69, 70, 103

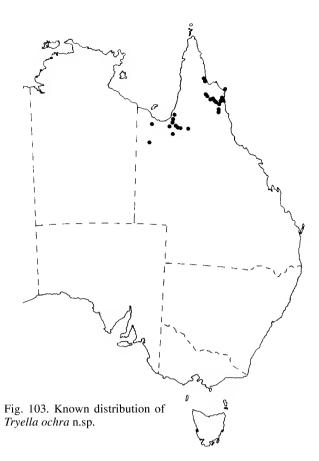
**Types**. Holotype ♂, K179894, Walkers Ck, 35 km NNE of Normanton, N Queensland, 2.i.1990, M.S. & B.J. Moulds, in AM. Paratypes as follows: QUEENSLAND— $2\delta\delta$ , 19, same data as holotype; all in **AE**.  $2 \stackrel{?}{\circ} \stackrel{?}{\circ}$ , K179895 and K179896,  $1 \stackrel{?}{\circ}$ , K179897, same data as holotype; all in AM. 13, 19, same data as holotype; 13, Silver Plains Homestead, Cape York Pens. 28.xi.1961, J.L. Wassell; all in ANIC. 2♂♂, 1♀, same data as holotype; all in ASCU. 2♂♂, 1♀, Walkers Ck, 35 km NNE of Normanton, N Queensland, 2.i.1990, MBM; all in BMNH. 233, 19, same data as holotype; all in JM. 2♂♂, 1♀, Walkers Ck, 35 km NNE of Normanton, N Queensland, 2.i.1990, MBM; all in **JO**. 2♂♂, 1♀, Walkers Ck, 35 km NNE of Normanton, N Queensland, 2.i.1990, MBM; all in LP. 2♂♂, 1♀, Walkers Ck, 35 km NNE of Normanton, N Queensland, 2.i.1990, MBM; all in MNHP. 1♂, 1♀, nr Thorntonia Hsd, 120 km ENE of Camooweal, 21.xii.1986, MBM; 1♀, Beames Brook, Burketown/Gregory rd jnct. 20.xii.1991, MBM; 1♂, Fitzmaurice Ck, N of Normanton, 3.i.1990, MBM; 134 ♂ ♂ (1 male genitalic preparation no. AB7), 58 ♀ ♀, Walkers Ck, 35 km NNE of Normanton, 16,18.xii.1986, 2,3.i.1990, 15.i.1992, MBM; 2 male, 2♀♀, Normanton, 15,17.i.1986, MBM; 699, Walkers Bend, Flinders R., 60 km SSW of Normanton, 14.i.1986, MBM; 2♂♂, 120 km S of Normanton, 14.i.1986, MBM; 1♂, 4♀♀, 28 km E of Croydon, 16.i.1986, MBM; 2♂♂, 6♀♀, 50 km SE of Normanton, 15.i.1986, MBM; 1♂, 17♀♀, East Haydon, 60 km SE of Normanton, 15.i.1986, MBM; 3♂♂, 80 km ESE of Normanton, 16.i.1992, MBM; 36 ♂ ♂ (1 male genitalic preparation no. AB5), 9 ♀ ♀, Morehead R. x-ing, 35 km S of Musgrave Hsd, Cape York Pen., 10.i.1988, 9.i.1990, MBM; 1&, 16 km SE of Hann R. x-ing, NW of Laura, 12.i.1990, MBM; 6♂♂ (1 male genitalic preparation no. AB57), Laura, 25.xii.1978, AMW-H; 3♂♂, 1♀, Little Laura R. via Laura, 24.xii.1978, R.I. Storey; 6♂♂ (1 male genitalic preparation no. AB56), 1♀, 35 km SE of Laura, 23.xii.1983, MBM; 2♂♂, Hells Gate Ck, S of Laura, 6.i.1981, GAD; 13♂♂ (1 male genitalic preparation no. AB6), 7♀♀, Mt Cook nr Cooktown, 31.xii.1983, MBM; 1♂, Archer Point near Cooktown, 7.i.1973, MBM; 1&, Black Mountain, S of Cooktown, 6.i.1981, MBM; 19, 23 km N of Palmer River, 14.i.1982, GAD; 1♂ (genitalic preparation no. AB49), 2♀♀, McLeod River x-ing NW of Mt Carbine, 7.i.1980, A. Hiller; 2♂♂ (1 male genitalic preparation no. AB8), 19, McLeod River x-ing NW of Mt Carbine, 11.i.1988, MBM; 1&, Station Creek, 15 km N of Mt. Molloy, 22.i.1981, MBM; 1 d, Station Ck, 10 km S of Mt Carbine, 28.i.1976, AMW-H; all in MSM. 3♂♂, 2♀♀, Silver Plains, Coen, 11,24.i.59, L. W[assell], Collection A.N. Burns; 2♂♂, 2♀♀, homestead, Silver Plains, east coast Cape York Pen., 3,7.xii.1959, at light, J.L. Wassell, Collection A.N. Burns; 1&, Clean Skin xing, Massy Creek, Silver Plains, east coast Cape York Pen., 8.i.60, J.L. Wassell, Collection A.N. Burns; all in MV.  $2\vec{\circ}\vec{\circ}$ ,  $1\vec{\circ}$ , same data as holotype; all in QM.  $2\vec{\circ}\vec{\circ}$ ,  $1\vec{\circ}$ , same data as holotype;  $2\vec{\circ}\vec{\circ}$ , Stewart R., i.-ii.1927, Hale & Tindale;  $1\vec{\circ}$ ,  $2\vec{\circ}\vec{\circ}$ , Flinders I., i.1927, Hale & Tindale; all in SAM.  $2\vec{\circ}\vec{\circ}$ ,  $1\vec{\circ}$ , same data as holotype; all in UQIC.  $2\vec{\circ}\vec{\circ}$ ,  $1\vec{\circ}$ , same data as holotype; all in WAM.

Other material examined. QUEENSLAND—2\$\displaystyle \displaystyle (teneral), homestead, Silver Plains, east coast Cape York Pen., 5.xii.1959, at light, J.L. Wassell, Collection A.N. Burns, in MV. 1\$\displaystyle 7\$, 7 km SE Mt Carbine, Mary R. camp, xii.1989, ANZSES Expedn, in QM. 1\$\displaystyle 3\$, Stewart R., i.-ii.1927, Hale & Tindale; 1\$\displaystyle 7\$, Flinders I., i.1927, Hale & Tindale, both in SAM.

**Etymology**. From the Greek *ochra* (feminine) meaning earthy oxide of iron and referring to the ochraceous colour on the pronotum of this species.

#### **Description**

Male (Figs. 27, 55a, 69, 70). Head. Either ferruginous with black behind eyes and partly below, or black with ferruginous postclypeus and anteclypeus. Rostrum brown becoming black towards apex; reaching hind coxae but not extending beyond their apices. Ocelli light amber to light ruby red. Eyes of live specimens (Gulf region) dark brown to black. Antennae brown or blackish on those individuals with brown heads, black on those with black heads. Underside of head (excluding postclypeus) with silverish pubescence, remainder with almost no pubescence. Thorax. Pronotum ochraceous, sometimes with dorsal midline darkened and ferruginous or tending so, this fascia spreading laterally both at its anterior and posterior ends, especially the latter; pronotal collar ferruginous or sometimes tending blackish on those individuals with dominantly brown heads, otherwise black (except for a small middorsal area and lateral margins) on those with black heads. Mesonotum ferruginous, sometimes with the dorsal region tending ochraceous which highlights a pair of subconical ferruginous fascia basal on anterior margin of pronotum; cruciform elevation of similar colour to adjoining dorsal area; a little golden-silver pubescence on some specimens principally along margins of wing grooves. Thorax below light brown with silverish pubescence. Wings. Hyaline. Fore wings usually without infuscations but some individuals with a narrow infuscation at base of apical cell 2, sometimes also at base of 3, and sometimes at distal end of apical cell 1; veins mostly blackish, costa ochraceous; basal cell translucent amber; basal membrane usually orange, sometimes discoloured brownish yellow; costa and veins on basal third or so usually bearing some silverish pubescence not always obvious to naked eye. Hind wings usually with a small black infuscation at distal extremity of vein 2A; whitish plaga on vein 2A extending full length, that on 3A not quite reaching to wing margin; much of anal lobe lightly suffused golden amber, especially on basal half; venation pale brown often becoming dark towards apex. Legs. Light ferruginous; without markings. Opercula. Light brown with a weak black suffusion; lateral margin usually edged black; for the most part sparsely covered by a silverish pubescence; clearly separated exposing apex of sternite I and barely concealing tympanal cavities. Abdomen. Tergites ferruginous; tending dark to nearly black towards anterior margin, and on some individuals narrowly edged pale cream along posterior margin of segment 3 and extending sometimes as far as 6. Sternites ferruginous; sternite II sometimes very dark and posterior margin of segments III-VI sometimes narrowly edged pale cream.



Usually bearing some fine silverish pubescence both dorsally and ventrally. *Tymbals* (Fig. 27). Usually 11 long tymbal ribs, otherwise as for generic description. *Genitalia* (Figs. 69, 70). Pygofer ferruginous; upper pygofer lobes in lateral view very broad at base, tapering gradually to a sharp upturned pointed apex, in ventral view angled inwards from near base; basal lobes without webbing fusing inner and outer lobes, outer lobe in lateral view like a very long thin finger, gently curved, almost as long as upper pygofer lobe. Uncal lobes scoop-like and gently upturned at their distal ends. Lateral processes of uncus in lateral view small and rounded. Conjunctival claws simple, sharply pointed, directed ventrally. Flabellum absent. Palearis on distal quarter of theca but not quite reaching the distal end, small and gradually tapering to zero at proximal end.

**Female** (Fig. 55b). Colour and markings similar to those of male. Abdominal segment 9 ferruginous, sometimes with diffused areas of black. Ovipositor sheath brown to black.

**Measurements.** n = 10 ♂ ♂, 10 ♀ ♀ (includes smallest and largest of available specimens). *Length of body*: male 15.2–18.5 (17.1); female 16.0–20.0 (18.2). *Length of fore wing*: male 21.1–25.4 (23.7); female 22.2–26.2 (24.3). *Width of head*: male 6.1–6.9 (6.4); female 6.1–7.1 (6.6). *Width of pronotum*: male 6.1–7.1 (6.6); female 6.1–7.4 (6.7).

Adult variability. Specimens from Cape York Peninsula south to the Palmer River all possess heads that are entirely black (except for the clypeus) and a predominantly black or nearly black pronotal collar; elsewhere specimens have ferruginous heads with black only behind the eyes and partly so below and a ferruginous or sometimes blackish pronotal collar.

**Distinguishing features.** This species is most similar to *T. castanea*, *T. burnsi* and *T. kauma*. In most cases individuals can be separated from those of the latter three species by having a light ochraceous pronotum, lack of or very reduced fore wing infuscations and a golden amber suffusion to the hind wing anal lobe. However, atypical specimens of *burnsi*, and *castanea* in particular, that closely resemble *ochra* are not uncommon and one should consult the *Key to species* or male genital structures for confirmation of identity. Care should also be taken not to confuse females of *ochra* with those of *T. lachlani*. The latter have a black cruciform elevation (unless teneral) and/or a dominantly ochraceous abdomen above; female *ochra* are never so coloured.

**Distribution** (Fig. 103). Northern Queensland from the lower Gulf region to northeastern Queensland between Coen and Mount Molloy. From the Gulf region there are records from as far west as the Burketown district and inland to Thorntonia Homestead some 120 km ENE of Camooweal. Far eastern Queensland records are primarily non-coastal although some specimens have been taken at Silver Plains and Flinders Island and near Cooktown.

It is sometimes a locally common species. There are records from early December to early February.

**Habitat**. Adults inhabit trees, particularly in the vicinity of water courses where they often perch high up among the smaller branches. Eucalypts are favoured.

**Song.** Singing occurs both during the day and at dusk; otherwise unknown.

# Tryella rubra (Goding & Froggatt, 1904), n.comb.

Figs. 13, 28, 62a-e, 79, 80, 104

*Tibicen ruber* Goding & Froggatt, 1904: 600–601; Hahn, 1962: 11; Stevens & Carver, 1986: 265.

Abricta ruber Distant, 1905b: 281; Distant, 1906: 130; Kirkaldy, 1907b: 308; Ashton, 1914: 349.

Abricta elseyi Distant, 1905b: 281; Distant, 1906: 130; Kirkaldy, 1907a: 16; Burns, 1957: 636; Metcalf, 1963: 207; Duffels & van der Laan, 1985: 234.

Abricta rubra Burns, 1957: 637; Metcalf, 1963: 209–210; Duffels & van der Laan, 1985: 235; Moulds, 1990: 121.

#### **Types**

(a) Tibicen ruber Goding & Froggatt. Lectotype male, designated by Moulds (1990), King's Sound (in ANIC, "on permanent loan from MM"). Examined.

(b) Abricta elseyi Distant. Syntype bearing four labels: (i) small blue grey circular label handwritten in black ink "north/austral"; (ii) white rectangular label handwritten in black ink "Abricta/elseyi/Dist./type"; (iii) small white circular label with red border on which is machine-printed "Type"; (iv) small white circular label with blue border on which is machine-printed "SYN-/TYPE" (in BMNH). Examined.

Distant (1905b) did not designate a holotype or state the number of specimens examined. While it is probable that he had only the one specimen listed above, following Recommendation 73F of the *Code* the specimen is retained as a syntype.

Material examined. Types and the following: WESTERN AUSTRALIA—1♀, Broome, 29.xii.1985, MBM; 1♀, Broome, 3.i.1990, A. Hay; 1♀, Fitzroy River crossing, Derby-Broome road, 3 xi.1978, MBM;  $2\delta\delta$ , 1, Fitzrov River, S of Derby, 7.ii.1989, S. Lamond; 1♂, Derby, 10.ii.1977, MBM; 6♂♂ (1 male genitalic preparation no. AB51), 299, 28 km S of Derby, 31.xii.1985, MBM; 2♂♂, 1♀, 21 km W of Penticost R. x-ing, Gibb R. Road, 30.xii.1991, MBM; 18, Telegraph Ck, 25 km N of Turkey Creek township, eastern Kimberleys, 3.i.1986, MBM; 900, 3 female, Kununurra, 7.i.1986, 27.xii.1991, 1.i.1992, MBM; 3♂♂, 2♀♀, Kimberley Research Stn., near Kununurra, 7.i.1986, MBM; all in MSM. NORTHERN TERRITORY—18, 299, Waterhouse River, Mataranka Hsd, 24.xii.1986, MBM; all in AE. 2♂♂, K179899 and K179900, 3♀♀, K179901-K179903, Waterhouse River, Mataranka Hsd, 24.xii.1986, MBM; all in AM. 13, 299, Waterhouse River, Mataranka Hsd, 24.xii.1986, MBM; all in ANIC. 1∂, 2♀♀. Waterhouse River, Mataranka Hsd, 24.xii.1986, MBM; all in BMNH. 13, 299, Waterhouse River, Mataranka Hsd, 24.xii.1986, MBM; all in JO. 1&, 2♀♀, Waterhouse River, Mataranka Hsd, 24.xii.1986, MBM; all in LP. 13, 299, Waterhouse River, Mataranka Hsd, 24.xii.1986, MBM; all in MNHP. 11 ♂ ♂, 3 ♀ ♀, Keep River x-ing, Victoria Hwy, 7.i.1986, MBM; 2 of of, West Baines R., Victoria Hwy, 8.i.1986, MBM; 13, 100 km WSW of Timber Creek, 6.ii.1977, MBM; 4♂♂, 6♀♀, Victoria R., 18 km W of Timber Creek township, 25.xii.1991, MBM; 1♂, Timber Creek, Victoria Hwy, 8.i.1986, MBM; 233 (one male genitalic preparation no. AB52), 19, 16 km W of Victoria River x-ing, Victoria Hwy, nr Fitzroy Rg, 9.i.1986, MBM; 1 d, old "Oolloo" x-ing, Daly R, 27.xi.1996, K.A. Kopestonsky; 133 d (2 male genitalic preparations Nos AB91, AB92), 129 9 Stuart Park, Darwin, 3,7,9.ii.1991, 5,9,27.xi.1991, 10.xii.1991 10,13,18,23,24,25,26,27.i.1992, 1,3.ii.1992, D.N. Wilson; 1& (genitalic preparation no. AB43), 12, Darwin, mid.xi.1983, R. Wood; 2♂♂, Berry Springs, 28.x.1993, 19.xi.1993, G.A. Husband; 1♀, Sth Alligator Riv., Arnhem Hwy, 11.xii.1981, A. Walford-Huggins; 13, 19 Springvale Stn, 12 km W of Katherine, 8.xii.1982, A. Walford-Huggins; 16 ♂ ♂ (one male genitalic preparation no. AB44), (one male figured "Aust. Cicadas" pl. 15, fig. 1), 499, Mainoru, ENE of Katherine, 22.xi.1981, 14.xii.1982, A. Walford-Huggins; 3 ₺ ₺, Koongarra, [nr Mt Broc kman], 29.xi,1978, at light, R.I. Storey; 69 ♂ ♂ (5 male genitalic preparations Nos AB53, AB74, AB75, AB76, AB77), 117 ♀ ♀, Waterhouse River, Mataranka Hsd, 9,10.i.1986, 23,24,25.xii.1986, 2.i.1987, MBM; 1♂, 1♀, Coolibah Ck, WNW of Top Springs 16°26'S 131°39'E, 24.xii.1991, MBM; 13, 27 km N of Daly Waters, 11.i.1986, MBM; 13, 19, 20 km E of Borroloola, 23.xii.1991, MBM; 5♂♂ (one male genitalic preparation no. AB93), Borroloola, 23.xii.1991, MBM; all in MSM. 1♂, 2♀♀, Waterhouse River, Mataranka Hsd, 23.xii.1986, MBM; all in QM. 19, Katherine, xii.1957, J. Wren, Collection A.N. Burns, in MV.  $1\delta$ , Katherine, 29.x.1975, G. Gow & P. Horner, in NTM. 299, Coomalie Ck, 27 km N Adelaide R., 28.ix.1977, G.F. Gross, J.A. Forrest; 1 \, Coomalie Ck, 50 km S Darwin, 28.ix.1977, G.F. Gross; 1 &, Groote Eylandt, (no date), N.B. Tindale; 1 &, 30 mi E Darwin, (no date), G.F. Hill; all in SAM. 399, 8 km NE by N of Mt Cahill, 12°48'S 132°44'E, 26.xi.1974, R.I. Storey; all in **UQIC**. 1♂, 2♀♀, Waterhouse River, Mataranka Hsd, 23.xii.1986, MBM; all in WAM.

# **Description**

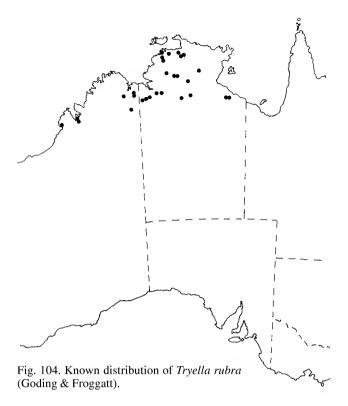
Male (Figs. 28, 62a,c, 79, 80). Head. Black with postclypeus ferruginous but some individuals almost entirely brown (the latter always black behind eyes and nearly always around ocelli). Often with a pale muddy-yellow blotch middorsally against posterior margin, this blotch never extending further than median ocellus. Anteclypeus ferruginous, reaching but not extending beyond their apices. Rostrum usually black dorsally and brown ventrally but sometimes almost entirely black or brown; reaching apices of hind coxae. Antennae often brown or partially so on basal segments 1 and 2, otherwise black. Head (excluding eyes and ocelli) usually covered to some extent with silver pubescence, especially so on underside. Thorax. Usually covered to some extent, sometimes substantially, with silver pubescence. Pronotum light to medium

ferruginous and nearly always with a distinct pale muddyyellow middorsal fascia that is slightly expanded against pronotal collar; pronotal collar dark brown to almost black. Mesonotum ferruginous, usually a little darker than pronotum; sometimes pale dorsally highlighting a pair of dark subconical markings based on anterior margin; cruciform elevation coloured similar to majority of dorsal surface. Thorax below ferruginous. Wings. Hyaline. Fore wings with or without dark brown infuscations, if present then confined to base of apical cell 2, and sometimes 3, and principally on cross veins, also sometimes in basal area of apical cell 1; venation brown with costa tending pale especially to node; basal cell weakly tinted translucent amber; basal membrane pale orange-brown but sometimes suffused grey, rarely orange; costa and veins on basal third or so sometimes bearing a little silver pubescence not always obvious to the naked eye. Hind wings with a heavy black infuscation on margin at distal end of vein 2A, often also with a less intense extension along margin of anal lobe no further than vein 3A, and rarely following along veins 2A and 3A; plaga yellowish white; under magnification majority of hind wing veins pale yellow with much of ambient vein blackish. Legs. Medium to light ferruginous; without markings. Opercula. Usually unicolourous, variable between individuals from light muddy-yellow to dark ferruginous; almost meeting and extending a little beyond tympanal cavities; normally covered by fine silver pubescence not always obvious to naked eye. Abdomen. Tergites ferruginous and usually bearing some silver pubescence. Sternites similar in colour to tergites, sometimes sternite II muddy-yellow, occasionally some other sternites with a pale muddy-yellow posterior margin. Tymbals (Fig. 28). Usually 10-11 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 79, 80). Pygofer dark ferruginous to mid brown, usually dark dorsally; upper pygofer lobe in lateral view straight, parallel-sided for most of length with rounded apex, in ventral view angled inwards from near base; basal lobes with outer and inner lobes of similar length and entirely fused by a broad webbing, in lateral view outer lobe tapering to a point confluent with webbing. Uncal lobes scoop-like and gently upturned at their distal ends; lateral processes of uncus in lateral view small and rounded. Conjunctival claws simple, sharply pointed, directed ventrally. Flabellum absent. Palearis absent.

**Female** (Figs. 13, 62b,d,e). Colour and markings similar to those of male. Abdominal segment 9 ferruginous brown, occasionally with a little black suffusion. Ovipositor sheath ferruginous brown to black.

**Measurements.** n =  $10 \ \frac{3}{6}$ ,  $10 \ \frac{1}{9}$  (includes smallest and largest of available specimens). *Length of body*: male 16.3–22.2 (19.0); female 17.6–22.3 (20.5). *Length of fore wing*: male 23.8–28.8 (26.0); female 23.6–29.6 (27.4). *Width of head*: male 6.6–8.4 (7.3); female 6.8–8.5 (7.7). *Width of pronotum*: male 6.6–8.8 (7.5); female 7.0–9.2 (8.1).

Adult variability. Individuals of *rubra* with heads entirely brown (excluding teneral individuals) tend to be smaller than average; all seven known specimens from the Borroloola district, NT, show this character but have typical *rubra* male genitalia. Other specimens, with entirely brown heads are known from Koongarra (just south of Jabiru) and from near Darwin, NT.



**Distinguishing features**. Typical individuals can be distinguished from other *Tryella* species by the pale mid dorsal pronotal stripe and black head. Atypical individuals can have either character absent but never both. Determination of such specimens can be obtained from the *Key to species*. The species most similar in overall appearance to *T. rubra* is *Aleeta curvicosta* which is readily distinguished on size, *rubra* never attaining a fore wing length of 31 mm and *curvicosta* always with a fore wing length exceeding 32 mm.

**Distribution** (Fig. 104). Northern Western Australia and the Top End of the Northern Territory from Broome to Borroloola. A lack of records from the inner Kimberley region and Arnhem Land is almost certainly an artifact of inadequate collecting.

It is sometimes a common species, but populations tend to rise and fall rapidly. Usually it is common around Kununurra, Western Australia, and I once encountered enormous numbers at Mataranka Homestead on the Waterhouse River, Northern Territory. Adults have been taken from late September to mid February but appear to be most common during late December and early January following the first summer rains.

**Habitat**. Adults inhabit eucalypts and other trees, usually growing in the vicinity of water courses. The upper branches are usually preferred so that adults are often beyond arm's reach.

**Song.** A vigorous and continuous rolling hiss-like sound sung both during the day and at dusk. Although groups of males sing together they do not sing in chorus. Males are capable of calling the morning following emergence. An analysis of the song is currently under study (Moulds, in prep.).

# Tryella stalkeri (Distant, 1907), n.comb.

Figs. 14, 29, 63a-d, 67, 68, 105

Abricta stalkeri Distant, 1907: 415; Ashton, 1914: 349; Burns, 1957: 637; Metcalf, 1963: 210; Duffels & van der Laan, 1985: 235; Moulds, 1990: 122, pl. 15, figs. 5, 5a.

Type. Lectotype  $\[ \]$  here designated and paralectotype  $\[ \]$  (in BMNH) (examined). Lectotype  $\[ \]$  (abdomen missing), bearing three labels: (1) "Nicol Bay/West Australia" handwritten in india ink; (2) "Distant Coll./1911-383" machine printed; (3) "Abricta stalkeri Dist" handwritten in india ink. Paralectotype  $\[ \]$ , bearing three labels: (a) "Alexandria/S. Australia/G.N. stalkeri/1907-261" handwritten in india ink; (b) "Abricta/stalkeri/Dist./type" handwritten in india ink; (c) a small circular label with red border with "Type" machine printed.

**Note.** The syntype male and female are not conspecific. To fix the identity of this species the female is chosen as lectotype in preference to the male so as to retain the accepted concept of the species. The paralectotype male is a specimen of *T. infuscata* n.sp.

Material examined. Types and the following: WESTERN AUSTRALIA—1∂, K179962, 19, K179963, Fortescue R., Hamersley Range, no date, W.D. Dodd, H. Ashton Coll.; 13, K179904, 19, K179905, De Grey R. crossing, 70 km E of Port Hedland, 6.iii.1984, at light, K. & E. Carnaby; all in AM. 16, Nanutarra Petrol Stn, 47 mi[les] NE of Barradale, 1.vii.1972, dead in spiders web, D. & N. McFarland, in ANIC. 19, Fortescue R., Hamersley Range, W.D. Dodd, in BMNH.  $10 \displayskip 3$  (1 male genitalic preparation no. AB50),  $10 \displayskip 9$ , De Grey R. crossing, 70 km E of Port Hedland, 6.iii.1984, at light, K. & E. Carnaby; 1033, 599, W Peawah River, 90 km SW of Port Hedland, 3.iii.1984, K. & E. Carnaby; 2♂♂, 1♀, Millstream, Fortescue River S of Roebourne, 22.ii.1977, MBM; 11♂♂, 1♀, (1♂, 1♀, figured "Aust Cicadas" pl. 15, fig. 5), Marble Bar, 17,18.ii.1977, MBM; 223 3 (2 male genitalic preparations Nos AB26, AB47), 4♀♀, Marble Bar, 3.ii.1972, 7.i.1973, 27.ii.1973, 13,18,28.i.1974, 3.i.1975, 1.i.1977, G.R. Jones; all in MSM.  $10 \stackrel{?}{\circ} \stackrel{?}{\circ}$ ,  $2 \stackrel{?}{\circ} \stackrel{?}{\circ}$ , Marble Bar, 8.ii.1973, 11.iii.1975, 27,28.xii.1975, 4.i.1976, G.R. Jones; 2♂♂, 1♀, Fortescue R., Hamersley Range, W.D. Dodd; all in SAM. 299, Dampier, 14.ii.1973, E.M. Exley; all in **UQIC**. 433, 499, reg. nos 34303-34310, Roy Hill, creek, i.[19]57, A. Douglas; 19, reg. no. 34315, Bamboo Creek, 20°56'S 120°13′E, 22.i.1974, A.M. & M.J. Douglas; 3♂♂, reg. nos 34312– 34314, Nullagine, 19-20.i.1974, A.M. & M.J. Douglas; all in WAM.

#### **Description**

**Male** (Figs. 29, 67, 68, 63a–c). *Head*. Usually mid to dark brown but on some individuals nearly black, often with a small indistinct ochraceous blotch on midline against posterior margin; postclypeus light to dark ferruginous; anteclypeus similar in colour to postclypeus. Rostrum ochraceous to brown, tending dark or even black towards apex but usually with extreme apex pale; passing bases, but not reaching apices, of hind coxae. Antennae brown to nearly black. Often bearing some silver pubescence, especially below. *Thorax*. Pronotum often light ochraceous but on some individuals medium to dark ferruginous; occasional specimens with a ferruginous fascia on dorsal midline, this fascia spreading laterally both at its anterior end against pronotal margin as far as eyes, and at its posterior end against pronotal collar; pronotal collar medium to dark brown sometimes tending black but usually paler anterior of lateral angles. Mesonotum medium to dark ferruginous, sometimes with a slightly paler ochraceous area between cruciform elevation and anterior margin which often accentuates an adjacent pair of obconical brown markings

based on anterior margin; cruciform elevation similar in colour to that dominating dorsal region of mesonotum. Thorax above often with some silver pubescence; below nearly always with an extensive silver pubescence. Wings. Hyaline. Fore wings always with a zigzag infuscation following basal veins of apical cells 2–4 and usually along the length of vein R1b forming apical cell 1; venation and costa light brown or yellowish; basal cell barely tinted brown; basal membrane similar to venation in colour. Hind wings with an infuscation at distal extremity of vein 2A against wing margin and sometimes also part way along the length of 2A; plaga off white; venation light brown or yellowish. Legs. Light brown to yellowish, without markings. Opercula. Muddy pale yellow to pale brown; almost meeting and barely concealing tympanal cavities; usually covered by fine silver pubescence not always obvious to naked eye. Abdomen. Tergites mid to dark brown, of even or nearly even tone but usually with tergite 2 paler laterally and tergite 8 darkened on posterior half with posterior margin narrowly edged black. Sternites mid to dark brown but often a broad band along midline darkest. Abdomen above and below often with silver pubescence not always obvious to naked eye. Tymbals (Fig. 29). Usually 10 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 67, 68). Pygofer ferruginous; upper pygofer lobes in lateral view very broad at base, gradually tapering to a blunt point or rounded apex, nearly straight, in ventral view angled inwards with division of terminal section not distinct; basal lobes without webbing fusing inner and outer lobes, outer lobe in lateral view like a very long thin finger, gently curved, not quite as long as upper pygofer lobe. Uncal lobes scoop-like and gently upturned at their distal ends; lateral processes of uncus in lateral view broad at base tapering to a thin rounded extremity. Conjunctival claws simple, sharply pointed, directed ventrally. Flabellum absent. Palearis on distal quarter of theca, the proximal end heavily chitinized as a small but prominent rounded lobe.

**Female** (Figs. 14, 63d). Colour and markings similar to male. Abdominal segment 9 similar in colour to abdomen, sometimes with dorsal beak darkened or nearly black. Ovipositor sheath usually darker than abdominal segment 9 and sometimes black or nearly so; clearly extending beyond dorsal beak.

Adult variability. The distinctive light ochraceous pronotum that contrasts with the darker head and mesonotum is found on specimens from all known localities. A darker form, which has the pronotum concolorous with the mesonotum, is known only from a series of specimens taken over a number of years at Marble Bar.

**Distinguishing features.** This species is most similar to *T. noctua* and *T. occidens*. Individuals with a pale pronotum are immediately distinguished by that feature. Individuals of uniform body colour differ from *noctua* and *occidens* by lacking black pigmentation on the hind wing adjacent to

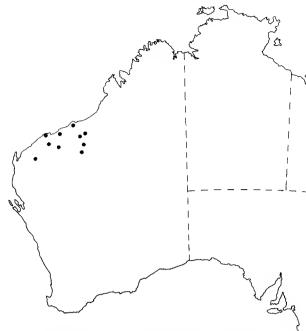


Fig. 105. Known distribution of Tryella stalkeri (Distant).

vein 3A. There is also some similarity to *T. crassa* but the fore wing infuscation of *stalkeri* reaches, or very nearly reaches, the top of 3rd ulnar cell whereas that of *crassa* does not approach anywhere near top of 3rd ulnar cell.

**Distribution** (Fig. 105). North-western Western Australia between the De Grey and Ashburton Rivers. There are records from Dampier (= Nickol Bay, type locality), Fortescue River at Millstream and near the Hamersley Rg, the Peawah River, Marble Bar and Nullagine. The species is locally common in some seasons. Adults have been taken from late December to mid March.

Distant (1907) records this species from Alexandria, Northern Territory, but this record almost certainly pertains to T. infuscata n.sp., q.v. Distant's mention of South Australia in regard to Alexandria stems from the fact that the Northern Territory was at the time under the administration of South Australia.

**Habitat**. Adults usually inhabit eucalypt trees, especially in the vicinity of watercourses, where the upper branches are often preferred.

#### Tryella willsi (Distant, 1882), n.comb.

Figs. 59a,b, 94, 95, 106

Tibicen willsi Distant, 1882: 127, pl. VII; Goding & Froggatt, 1904: 609.

Abricta willsi Distant, 1905a: 27; ibid., 1906: 131; Froggatt, 1907: 351; Kirkaldy, 1907b: 308; Ashton, 1914: 349; Kato, 1932: 181; Burns, 1957: 637; Metcalf, 1963: 210; Wagner, 1968: 155; Duffels & van der Laan, 1985: 235; Moulds, 1990: 123–124; Ewart, 1993: 139.

#### **Types**

(a) Lectotype female here designated and 2 paralectotype females (in BMNH) (examined). Lectotype  $\mathcal{P}$  bearing five labels: (i) "Peak Downs." handwritten in india ink; (ii)

There are also  $2\delta \delta$  in BMNH labelled "Peak Downs", "Distant Coll./1911-383" that have been previously considered syntypes of *willsi*. Distant (1882) clearly had only females (except for a male in ZMH discussed below) so these specimens cannot be syntypes of *willsi* and are here disregarded.

(b) Paralectotype male and paralectotype female (in ZMH) (examined). Paralectotype  $\delta$  bearing four labels: (i) "Sidney[sic]./Mus. Godeffroy./No. 17625" machine printed with 17625 handwritten in india ink; (ii) label with bold black printed border, a fine inner printed border within which "No." is machine printed at the top left hand corner and "Museum Godeffroy/Hamburg" between the borders at top and bottom respectively, and handwritten inscription in india ink "17625./Tibicen./willsi./ Sidney/Dist" (possibly the oldest label); (iii) label with printed black border within which is handwritten "W. willsi Dist."; (iv) pink label on which is machine printed "Paratype". Paralectotype ♀ bearing three labels: (i) "Peak Downs" handwritten, "Mus Godeffroy./No." machine printed, "17625" handwritten; (ii) label with bold black printed border, a fine inner printed border within which "No." is machine printed at the top left hand corner and "Museum Godeffroy/Hamburg" between the borders at the top and bottom respectively, and handwritten inscription in india ink "17625./ Tibicen./willsi./PK Downs/Dist." (possibly the oldest label); (iii) pink label on which is machine printed "Paratype."

Lectotype and paralectotype designations. Distant (1882) based his description of this species on nine females but added a footnote stating that "[Since writing the above I have discovered one male specimen of this species in the Godeffroy collection, which was received from Sydney...]". Under Article 72.4.1 of the *Code* this male could be considered to form part of the type series and that Wagner (1968) correctly listed this male (plus a female) in ZMH as syntypes. All six syntypes are conspecific. I am reluctant to designate the single male as a lectotype because it could be argued by some that it does not form part of the type series. The female selected as lectotype has been so chosen because it is typically coloured and is here designated so as to clarify the identity of this species.

Type locality. Distant (1882) lists Peak Downs and Sydney as type localities. Only the male in ZMH is labelled as coming from Sydney. Distant's footnote to the original description states that this male "was received from Sydney" and it appears likely that Distant assumed it originated from Sydney. As it is conspecific with the 5 known females, and the known distribution of the species is restricted to Queensland, it is reasonable to consider this male incorrectly labelled and that Sydney is an erroneous locality.

Material examined. Types and the following specimens: OUEENSLAND—8♂♂, K179906–K179913, 8♀♀, K179987–K179994 "Separation" nr Duaringa, xii.1993–iv.1994, A.W. Smith; 2 ♀ ♀, K179958, K179959, Carnarvon Rge, 14.xii.1948, N. Geary; all in AM. 1 d., 10 km W of Undilla Hsd, 95 km ENE of Camooweal, 21.xii.1986, MBM; 2♀♀, nr Undilla Hsd, 60 km ENE of Camooweal, 21.xii.1986, MBM; 1&, Selwyn Mine, 160 km SE of Mt Isa, 30.i.1991, T. Woodger;  $3 \stackrel{?}{\circ} 3$ ,  $2 \stackrel{?}{\circ} 2$ , Nonda railway stn, 70 km W of Richmond, 6.i.1987, MBM; 5♂♂, 1♀, 30 km N of Hughenden, 21.i.1977, MBM; 10♂♂ (1 male genitalic preparation no. AB54), 34 \ \ \ \ \ , 60 km E of Hughenden, 4.ii.1981, MBM; 1&, Sheepskin Ck, [nr Connors R.], 75 mi SSW of Sarina, 10.xi.1973, AMW-H; 1♂, Barcaldine, 10.ii.1981, MBM; 6♂♂, 2♀♀, "Noonbah", SW of Longreach, 27,28,31.i.1998, 1,2,4,5,6.ii.1998, A. Emmott; 2 of of A. 40 km SE of Blackall on Barcoo R., 30.xii.1993, J.E. & M.S. Heath; 20♂♂, 96♀♀, Barcoo R, S of Blackall, 24°35'01"S 145°48'31"E, 29.xii.2000, MBM; 1♀, Bee Ck, 25 km SW of Nebo, 6.ii.1981, MBM;  $2 \stackrel{?}{\circ} \stackrel{?}{\circ}$ ,  $3 \stackrel{?}{\circ} \stackrel{?}{\circ}$ , 60 km NE of Clermont, 7.ii.1981, MBM; 1♂, 6♀♀, 100 km NW of Marlborough, 28.i.1981, P.S. Valentine; 299, Grave Gully, approx. 40 km N of Marlborough, 3.ii.1973, AMW-H; 1♀, 2 km W of Emerald, 1.i.1994, J.E. & M.S. Heath; 7♂♂, 13♀♀, "Mourangee", near Edungalba, on red soil tableland, 14.xi.1987, E.E. Adams; 1♂, 3♀♀, Mourangee Hsd, near Edungalba, 18.xii.1985, R. Adams; 13, 3.5 km N of Mourangee Hsd, near Edungalba, 7.xi.1986, E.E. Adams; 5♂♂, 2♀♀, same data but 4 km N and 20,23.i.1991; 19, same data but 3 km E and 28.i.1991; 1, same data but 5 km E and 5.xii.1983; 3, 3, 4, 9, same data but 4 km SE and 28.i.1991; 9♂♂, 7♀♀, same data but 5 km S and 14.xii.1983, 11,28.xi.1987; 2♂♂ (1 male genitalic preparation no. AB55), 19, same data but 5 km SW and 24.xii.1983; 299, same data but 2 km WNW and 6.xi.1986; 19, "Bellwood", near Edungalba, 25.xii.1983, E.E. Adams; 21 ♂ ♂, 10 ♀ ♀, foothills of Blackdown Tableland, Expedition Range, 23.xii.1972, MBM; 1♀, Springsure, 28.xii.1995, D. Kitchin and T. Jack; 2♀♀, 6 km NE of Rolleston, 24.xi.1986, MBM; 13, 65 km S of Rolleston, 20.xii.1983, MBM; 3♀♀, Charleville, 19.xii.1995, Colin Dollery; 19, Biloela, 21.xii.1995, D. Kitchin, T. Jack; 18, Theodore, 16.i.1991, GAD; 7 o o (1 male genitalic preparation no. AB81), 499, Mt Scoria, near Thangool, 21.xi.1987, R. Eastwood; 533 2♀♀, 49 km SSE of St George near Moonie R., 18.xii.1983, MBM; all in MSM. 19, 60 km E of Hughenden, 4.ii.1981, MBM; 19, Hughenden, (no date), H.H. Batchelor; all in QM. 19, Cloncurry, 7.ii.1966, P. Brown; 19, Biloela, 12.i.[19]47, A.R. Bird; 18, Linville, 16.xii.[19]51, G. Saunders; 2♂♂, 2♀♀, 28 km ENE of Eulo, 28°04'S 145°18'E, 16.iii.1991, C.J. Burwell; all in UQIC.

#### Description

Male (Figs. 59a, 94, 95). Head. Black; postclypeus dark reddish brown; anteclypeus black, sometimes with a hint of brown. Rostrum brown at base becoming black apically; passing bases but not apices of hind coxae. Ocelli amber to ruby red. Antennae black. Head above lacking obvious pubescence, below usually with silver pubescence primarily on lorum and not always obvious to naked eye. Thorax. Pronotum orange yellow with a broad black fascia on midline, this fascia spreading laterally both at its anterior end against pronotal margin and at its posterior end against pronotal collar; pronotal collar black but sometimes brown anterior or lateral angles; anterior and posterior oblique fissures strongly mottled black or dark brown. Mesonotum usually black but sometimes dark ferruginous but always with a large black blotch immediately anterior of cruciform elevation and along lateral margin above wing bases; cruciform elevation either black or mid brown. Thorax above without noticeable silver pubescence. Thorax below partly black and partly brown but always brown adjacent to legs and usually bearing fine silver pubescent not obvious to naked eye. Wings. Hyaline. Fore wings with distinct infuscations at bases of apical cells 2 and 3 and sometimes also extending to cell 1, the infuscations at bases of cells 2 and 3 usually a continuous zigzag but occasionally

divided into two; venation brown to black, costa ochraceous usually with costal vein brown; basal cell always partly or entirely tinted translucent brown; basal membrane orange; costa and veins on basal third or so occasionally bearing some silver pubescence not visible to naked eve. Hind wings usually with a distinct infuscation at distal end of vein 2A; plaga light brown often with a dark tinge either side of plaga on 3A and a very weak brownish tinge barely discernible principally over basal half; venation brown. Legs. Brown, sometimes partly tending black, without markings. Opercula. Light vellowish brown contaminated to varying degrees by black suffusion; usually carrying some silver pubescence usually not discernible to naked eye; clearly separated exposing apex of sternite I and barely concealing tympanal cavities. Abdomen. Tergites black or nearly so, the posterior margin of segments 2–7 ochraceous or ferruginous, tergite 8 black to varying degrees but always substantially black dorsally and usually substantially ferruginous laterally. Sternites ferruginous; posterior margin of III-VI ochraceous; midline of sternites with a distinct, but not sharply defined, black fascia. Abdomen above and below often with some silver pubescence but usually not obvious to naked eye. Tymbals. Usually 10–11 long tymbal ribs, otherwise as for generic description. Genitalia (Figs. 94, 95). Pygofer black or brown and black; upper pygofer lobes in lateral view with upper margin distinctly curved outwards in central region, lower margin straight with distal end curved upwards towards an upturned pointed apex, in ventral view angled slightly inwards near midpoint and outwards on distal quarter; basal lobes with a broad webbing fusing much of outer and inner lobes, in lateral view outer lobe just a short finger-like projection beyond webbing. Uncal lobes scoop-like and gently upturned at their distal ends; lateral processes of uncus in lateral view nearly equal in length to upper pygofer lobes, straight, parallel-sided, apex nearly square. Conjunctival claws simple, sharply pointed, directed laterally. Flabellum a large rounded lobe across entire ventral surface. Palearis near distal end of theca, rounded with proximal end gradually tapering.

**Female** (Fig. 59b). Colour and markings similar to male. Abdominal segment 9 dark ferruginous brown tending black; always black dorsally including dorsal beak. Ovipositor sheath black and clearly extending beyond dorsal beak.

**Measurements**. n = 10 ♂ ♂, 10 ♀ ♀ (includes smallest and largest of available specimens). *Length of body*: male 15.3–19.2 (17.9); female 16.5–21.8 (19.9). *Length of fore wing*: male 20.4–24.3 (23.0); female 21.9–26.5 (24.9). *Width of head*: male 5.4–6.2 (5.9); female 5.5–6.8 (6.3). *Width of pronotum*: male 5.5–6.6 (6.2); female 5.7–7.1 (6.7).

**Distinguishing features**. This is clearly the blackest of all *Tryella* species and typical specimens are unlikely to be misidentified. However, a series of three males and two females from Nonda in the central west of northern Queensland, show a basic ferruginous pigmentation rather than black and slightly reduced fore wing infuscations so that they are indistinguishable from *T. burnsi* without reference to male genitalia. Even then care must be taken in assessing characters; the presence of a well-developed palearis on the aedeagal theca of *willsi* clearly distinguishes this species from *burnsi*. The known distributions of these two species are, for the most part, allopatric but they may

be possibly sympatric in coastal districts between Mackay and Rockhampton although all known records for the two species in this region are separated by the Connors Range, *willsi* occurring only to the west and *burnsi* only to the east.

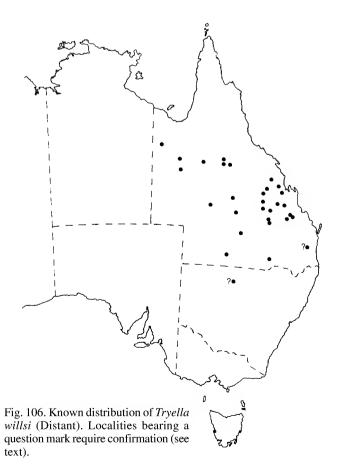
Aberrant specimens might also be confused with *T. graminea* but are at once distinguished by the glass-clear wings of *willsi* compared to the slightly tinted wings of *graminea* (clearly visible when held above a white background).

Distribution (Fig. 106). Inland Queensland from Undilla Stn near Camooweal in the north-west of the State to near Eulo (Burwell, 1991) and St George in the south and possibly to Bourke in northwestern NSW (Goding & Froggatt, 1904). To the east it extends to near Hughenden, the Isaac River, Mt Scoria near Thangool and possibly to Linville although the latter requires confirmation. Western limits in central Queensland include Blackall and the Rolleston/Injune road near Carnarvon Gorge. Adults are sometimes locally common. There are records from early November to mid February.

The distribution for this species given by Moulds (1990) includes records of *T. burnsi* n.sp. unrecognized at the time as a separate species. Records of *T. willsi* from Sydney (Distant, 1882) and King's Sound (Goding & Froggatt, 1904) are considered erroneous.

**Habitat**. Shrubs and small trees, especially eucalypts and often *Acacia* species, including brigalow (*A. harpophylla*).

**Song.** A continuous hissing call sung both during the day and at dusk; otherwise unknown.



ACKNOWLEDGMENTS. I am especially grateful to Dr M. Coombs and Dr H. Duffels for reviewing the final manuscript and providing many constructive comments. For comments on earlier drafts I am also most grateful to Dr M. Fletcher, Dr M. Gray, Prof. D.F. Hales and Dr D.K. McAlpine.

A number of collectors have provided specimens that have added distribution records or helped resolve taxonomic problems. In particular I wish to thank Ernest Adams, Graham Brown, Edie and her late husband Keith Carnaby, Greg Daniels, Rod Eastwood, Angus Emmott, Jack and Sue Hasenpusch, Shiela Hunter, the late Gordon Jones, Rob Lachlan, David Lane, John Olive, Allan Walford-Huggins, Geoff Williams and Terry Woodger.

The following people have kindly provided access to specimens in their care: Dr N.M. Andersen, UZMC; Prof. M. Boulard, MNHP; Dr M. Carver, ANIC; Prof. A. Ewart, Brisbane; Ms J. Forrest, SAM; Mr L.R. Greenup, Sydney; Dr T. Houston, WAM; Dr M. Humphrey and Dr D.S. Horning, MM; Ms C. McPhee, MV; Mrs J. Margerison-Knight, BMNH; Dr G.B. Monteith, QM; Dr J. Moss, Brisbane; Dr M. Schneider, UQIC; Mr R. Storey, DPI, Mareeba; Prof. H. Strümpel, ZMH; Dr K. Walker, MV; Mr M.D. Webb, BMNH and Dr A. Wells, NTM.

Geoff Avern, AM, gave guidance with photomicroscopy and provided the electron micrographs (Figs. 7–14, 18–29). For the photographs used in the coloured figures I extend my thanks to Cizary Rojewski. I am especially grateful to Kyra Kopestonsky for drawing Figs. 1–2, 5–6, 31–32, 35–38, 42–45 and to Alexandra De Laurentiis for the tracing and inking of Figs. 33–34, 46–49, 67–74, 79–86, 92–101.

In addition I wish to thank Geoff Avern, Sally Cowan, David Hain, Shane McEvey and Geoff Williams who have assisted in a variety of ways. The contribution of each is greatly appreciated.

For assistance with cladistic analyses I thank Drs M. Gray (AM) and D. Yeates (UQ). I am indebted also to the librarians and staff of the Australian Museum, Sydney; The Natural History Museum, London; CSIRO, Black Mountain Laboratories, Canberra and North Carolina State University, Raleigh, for access to literature.

For collecting permits I thank National Parks and Wildlife Service, NSW; Forestry Commission of NSW; National Parks, Northern Territory; Department of Forestry, Queensland, and National Parks and Wildlife Service, Queensland.

My wife Barbara and son Timothy have also played a major role in field work, including several trips to remote areas. I also thank Barbara for typing the manuscript.

#### References

- Anonymous, 1948. *Insect Pest Survey for the Year Ending 30th June, 1948.* (2nd Annual Report). Entomological Branch, Division of Science Services, N.S.W. Department of Agriculture. Pp. i-ii, 1-30.
- Ashton, H., 1912. Catalogue of the Victorian Cicadidae in the National Museum, Melbourne. *Memoirs of the National Museum of Victoria* 4: 23–29, pl. IV. [Separate paginated 1–7]
- Ashton, H., 1914. Catalogue of the Cicadidae in the South Australian Museum with descriptions of several new species. *Transactions and Proceedings of the Royal Society of South Australia* 38: 345–358, pl. XVII.
- Ashton, H., 1915. Synonymic notes on a recent catalogue of Cicadidae in the South Australian Museum. *Transactions of the Royal Society of South Australia* 39: 91.
- Atkinson, E.T., 1885. Notes on Indian Rhynchota, No. 4. *Journal of the Asiatic Society of Bengal* 54: 127–158.
- Atkinson, E.T., 1886. Notes on Indian Rhynchota, no. 6. Addenda and index. *Journal of the Asiatic Society of Bengal* 55: 143–223.
- Bailey, L.H., Bailey, E.Z. et al., 1976. Hortus Third. A Concise Dictionary of Plants Cultivated in the United States and Canada. Macmillan, New York and Collier Macmillan, London. xiv, 1290 pp.
- Bennett, G., 1860. Gatherings of a Naturalist in Australia; Being Observations Principally on the Animal and Vegetable Productions of New South Wales, New Zealand, and Some of the Austral Islands. John van Voorst, London. Pp. i–xii, 1–456. [Cicadas pp. 270–273, 313] [Facsimile reprint 1982, Currawong Press, Milson's Point, NSW]
- Boisduval, J.A., 1835. Voyage de découvertes de l'Astrolabe exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M. J. Dumont D'Urville. Faune entomologique de l'Océan Pacifique, avec l'illustration des Insectes nouveaux recueillis pendant le voyage. Vol. 2, Coléoptères et autres Ordres. J. Tastu, Paris. Pp. i–vii, 1–716, pls. 1–12. [Cicadas pp. 609–622; pl. 10]
- Boulard, M., 1979. Révision de la faune cicadéenne des Iles Maurice et Rodriguez. *Bulletin de la Société entomologique de France* 84: 27–47.
- Boulard, M., 1980. Cicadoidea nouveaux de l'Afrique sudorientale (Hom.). *Bulletin de la Société entomologique de France* 85: 165–173, pl. 1.
- Boulard, M., 1988. Homoptères Cicadoidea de Nouvell-Calédonie. 1. Description d'un genre nouveau et de deux espèces nouvelles de Tibicinidae. In *Zoologia Neocaledonica, volume 1*, ed. S. Tillier. *Mémoires de la Muséum National d'Histoire Naturelle, Paris* (A)142: 61–66.
- Boulard, M., 1990. Contribution l'entomologie générèle et appliquee. 2. Cicadaires (Homoptères Auchenorhynques). Première partie: Cicadoidea. *Ecole pratique des hautes Etudes, travaux du Laboratoire Biologie et Évolution des Insectes Hemipteroidea* 3: 55–245, pls. 5–26.
- Boulard, M., 1991. Cigales colligées lors des "Voyages de découvertes" conduits par J. Dumont d'Urville. Description de Poecilopsaltria durvillei, n. sp. (Hom. Cicadoidea, Cicadidae). Bulletin de la Société entomologique de France 96(2): 117–124.
- Boulard, M., 1996. Les cigales de la France méditerranéene (généralités et particularités). In *Vies & Mémoires de Cigales Provence Languedoc Méditerranée*, ed. M. Boulard & B. Mondon, pp. 5–72.
- Burmeister, H.C.C., 1835. Schnabelkerfe. Rhynchota. *Handbuch der Entomologie*. von Reimer, Berlin. 2(1): 1–396.
- Burns, A.N., 1957. Check list of Australian Cicadidae. Entomologischen Arbeiten aus dem Museum Georg Frey 8(2): 609-678.
- Burns, A.N., 1958. The genus *Diemeniana* Distant with description of a new species (Hemiptera-Homoptera, Cicadidae, Tibicininae). *Proceedings of the Royal Society of Victoria* 70(2): 145–161, pl. XXV.

- Burwell, C.J., 1991. New distribution records of three Queensland cicadas (Homoptera: Cicadidae). *Australian Entomological Magazine* 18(3): 124.
- China, W.E., 1929. A new genus of Cicadidae (Homoptera) from Angola. Annals and Magazine of Natural History (10)3: 426–428.
- Chisholm, E.C., 1932. The identity of *Psaltoda harrisi* and that of a near ally. *Australian Naturalist* 8(7): 131–134.
- Clyne, D., 1990. Insects. In *Urban Wildlife of New South Wales*, ed. J. Pastorelli, pp. 112–135, colour figure p. 108. Collins/ Angus & Robertson, North Ryde.
- Dallas, W.S., 1867. Insecta. *Zoological Record* 3: 558–561, 565, 567, 569, 571–573.
- Delétang, L.F., 1923. Monografia de los Cicadidos (Cicadidae) argentinos y relacion de estos con la fauna sudamericana. *Anales del Museo Nacional de Historia Natural Buenos Aires* 31: 538–649.
- Distant, W.L., 1882. On some undescribed Cicadidae from Australia and the Pacific region. *Proceedings of the Zoological Society of London* 1882: 125–134, pl. 7.
- Distant, W.L., 1883. Rhynchota: Homoptera. In *Biologia Centrali-Americana: contributions to the knowledge of the fauna and flora of Mexico and Central America*, ed. F.D. Godman & O. Salvia. Vol. 1, no. 23, pp. 17–24, col. pl. 3. R.H. Porter, London.
- Distant, W.L., 1892a. *A Monograph of Oriental Cicadidae*. Indian Museum, Calcutta. Parts 5–7: i–xiv, 97–158, pls. x–xv.
- Distant, W.L., 1892b. On some undescribed Cicadidae, with synonymical notes. Annals and Magazine of Natural History (6)9: 313–327.
- Distant, W.L., 1905a. Rhynchotal notes.—XXXIII. Annals and Magazine of Natural History (7)16: 22–35.
- Distant, W.L., 1905b. Rhynchotal notes.—XXXV. Annals and Magazine of Natural History (7)16: 265–281.
- Distant, W.L., 1906. A Synonymic Catalogue of Homoptera. Part 1. Cicadidae. British Museum, London. Pp. 1–207. [Reprinted 1966, Johnson Reprint Corp., New York]
- Distant, W.L., 1907. Rhynchotal notes.—XLIII. Annals and Magazine of Natural History (7)20: 411–423.
- Distant, W.L., 1913. Undescribed species of Cicadidae. *Annals and Magazine of Natural History* (8)12: 485–491.
- Distant, W.L., 1915. On some Australian Cicadidae. *Annals and Magazine of Natural History* (8)16: 50–53.
- Distant, W.L., 1920. Rhynchota from New Caledonia. Part II. Homoptera. Annals and Magazine of Natural History (9)6: 456–470
- Dlabola, J., 1962. Descriptions of new species of cicadids from Central Africa (Homoptera) (Cicadidae). Revue de Zoologie et de Botanique Africaine 65(1-2): 59-61.
- Dlabola, J., 1971. Eine neue afrikanische *Trismarcha*-Art (Homoptera, Cicadoidea). *Acta Entomologica Musei Nationalis Pragae* 38: 151–153.
- Dohrn, F.A., 1859. Catalogus Hemipterorum. Entomologischen Verein zu Stettin, Stettin. 112 pp. [Cicadas pp. 56–93]
- Donovan, E., 1820. Cicada. In: *The Cyclopaedia; or, Universal Dictionary of Arts, Science and Literature*, A. Rees, 8: [1–7].
- Duffels, J.P., 1977. A revision of the genus *Diceropyga* Stål, 1870 (Homoptera, Cicadidae). *Monografieën van de Nederlandsche Entomologische Vereeniging* 8: 1–227.
- Duffels, J.P., 1983. Taxonomy, phylogeny and biogeography of the genus *Cosmopsaltria*, with remarks on the historic biogeography of the subtribe Cosmopsaltriaria (Homoptera: Cicadidae). *Pacific Insects Monograph* 39: 1–127.
- Duffels, J.P., & P.A. van der Laan, 1985. Catalogue of the Cicadoidea (Homoptera, Auchenorhyncha) 1956–1980. Series Entomologica, vol. 34, 414 pp. Junk, Dordrecht, Netherlands.
- Dugdale, J.S., [1972]. Genera of New Zealand Cicadidae [Homoptera]. New Zealand Journal of Science 14(4): 856–882.

- Dworakowska, I., 1988. Main veins of the wings of Auchenorrhyncha (Insecta, Rhynchota: Hemelytrata). Entomologische Abhandlungen und Berichte aus dem Staatlichen Museum für Tierkunde in Dresden 52(3): 63–108.
- Ewart, A., 1990. Status of the Germar and Leach types of Australian cicadas (Homoptera) held at the Hope Entomological Collections, Oxford. *Australian Entomological Magazine* 17(1): 1–5.
- Ewart, A., 1993. Cicadas of the Heathlands region, Cape York Peninsula. In *Cape York Peninsula Scientific Expedition Report* 2. Royal Geographical Society of Queensland Inc. Pp. 135–147.
- Ewart, A., 1995. Cicadas. In *Wildlife of Greater Brisbane*, ed. M. Ryan, pp. 79–88. Queensland Museum, Brisbane.
- Ewart, A., 2001a. Dusk chorusing behaviour in cicadas (Homoptera: Cicadidae) and a male cricket, Brisbane, Queensland. *Memoirs of the Queensland Museum* 46: 499–510.
- Ewart, A., 2001b. Emergence patterns and densities of cicadas (Hemiptera: Cicadidae) near Caloundra, south-east Queensland. *Australian Entomologist* 28: 69–84.
- Fabricius, J.C., 1798. Entomologia systematica emendata et aucta secundum classes, ordines genera, species adiectis synonymis, locis, observationibus, descriptionibus. Supplementum. Ryngota. Os Rostro; Vagina articulata. Pp. 511–524. Proft, Copenhagen (Hafniae).
- Fabricius, J.C., 1803. Systema rhyngotorum secundum ordines, genera, species, adiectis synonymis, locis, observationibus, descriptionibus. 314 pp. [Includes an alphabetical index with separate pagination, 1–21]
- Farris, J.S., 1989. *Hennig86 Reference. Version 1.5.* 19 pp. Privately published by the author.
- Finlayson, H.H., 1934. Note on the swarming and metamorphosis of a Central Australian cicada, *Thopha colorata* (Distant). *Transactions of the Royal Society of South Australia* 58: 232–233.
- Fleming, C.A., 1975. Adaptive radiation in New Zealand cicadas. *Proceedings of the American Philosophical Society* 119(4): 298–306.
- Froggatt, W.W., 1903. Cicadas ("locusts") and their habits. *Agricultural Gazette of New South Wales* 14(5): 418–425. [Reprinted, Miscellaneous Publication 643: 1–8, pl. 2]
- Froggatt, W.W., 1907. *Australian Insects*. William Brooks, Sydney. 449 pp., 37 pls.
- Froggatt, W.W., 1914. The insects of New South Wales. *Handbook for New South Wales*. British Association for the Advancement of Science 84th Meeting, Australia. Pp. 330–347.
- Froggatt, W.W., 1933. *The Insect Book*. Shakespeare Head Press, Sydney. 103 pp., illustr. [Reprinted in 2nd edition, 1936]
- Germar, E.F., 1830. Species Cicadarium enumeratae et sub genera distributae. *Thon's Entomologisches Archiv* 2(2): 37–57, pl. 1.
- Germar, E.F., 1834. Observations sur plusieurs espšces du genre Cicada, Latr. *Revue Entomologique*, *Silbermann* 2: 49–82, pls. 19–26.
- Goding, F.W., & W.W. Froggatt, 1904. Monograph of the Australian Cicadidae. Proceedings of the Linnean Society of New South Wales 29(3): 561–670, pls. XVIII, XIX.
- Hahn, D.E., 1962. A List of the Designated Type Specimens in the Macleay Museum. Insecta. Macleay Museum, University of Sydney. 184 pp.
- Handlirsch, A., 1925. Ordung: Homoptera (Latr.) Westw. (Homopteren) in Systematische sbersicht (Schluss.). Schroder's Handbuch der Entomologie 3(17–18): 1102–1126.
- Hardy, G.H., 1918. Tasmanian Cicadidae. *Papers and Proceedings of the Royal Society of Tasmania* 1917: 69–71.
- Henderson, R.J.F. (ed.), 1997. *Queensland Plants: Names and Distribution*. Department of Environment, Brisbane. 286 pp.

- Hockings, F.D., 1980. Friends and Foes of Australian Gardens (Including Pests, Diseases, Parasites and Predators). A.H. & A.W. Reed, Sydney. 151 pp.
- Karsch, F.A.F., 1890. Beiträge zur Kenntniss der Singcikaden Afrika's und Madagaskar's. Berliner Entomologische Zeitschrift 35: 85-130, pls. III-IV.
- Karsch, F.A.F., 1891. Neue Singcicaden Kamerun's gesammelt von Herrn Dr. Paul Preuss. *Entomologische Nachrichten* 17: 347–352.
- Karsch, F.A.F., 1893. Neue Singcicaden von Victoria in Kamerun, gesammelt von Herrn Dr. Paul Preuss. Entomologische Nachrichten 19: 170–173.
- Kato, M., 1932. Monograph of Cicadidae. San Sei Do, Tokyo. 450 pp., 32 pls. [In Japanese but partly supplemented by English]
- Kato, M., 1956. *The Biology of Cicadas*. 319 pp, 46 pls. Iwasaki Shoten, Jinbocho Kanda, Tokyo. [In Japanese; headings, subheadings, captions and index in English]
- Kirby, W.F., 1893. Rejoinder to Dr. Bergroth and Mr. Distant. Wiener Entomologische Zeitung 12: 176–180.
- Kirkaldy, G.W., 1904. Bibliographical and nomenclatorial notes on the Hemiptera.—No. 3. *Entomologist* 37: 279–283.
- Kirkaldy, G.W., 1907a. Leaf-hoppers—supplement. (Hemiptera.) Hawaiian Sugar Planters' Association, Division of Entomology Bulletin 3: 1–186, pls. 1–20.
- Kirkaldy, G.W., 1907b. Some annotations to M. Distant's recent Catalogue of the Cicadidae. [Hem] (1). *Annales de la Société entomologique de Belgique* 51: 303–309. [Separate paginated 1–7]
- Kramer, S., 1950. The morphology and phylogeny of auchenorhynchous Homoptera (Insecta). *Illinois Biological Monographs* 20(4): i-vii, 1–111.
- Kuhlgatz, T., 1905. Schadliche Wanzen und Cicaden der Baumwollstauden. Mitteilungen aus dem Zoologischen Museum, Berlin 3: 31-115, pls. 2-3.
- Kukalová-Peck, J., 1983. Origin of the insect wing and wing articulation from the arthropodan leg. *Canadian Journal of Zoology* 61: 1618–1669.
- Mac Nally, R.C., & J.M. Doolan, 1986a. Patterns of morphology and behaviour in a cicada guild: a neutral model analysis. *Australian Journal of Ecology* 11: 279–294.
- Mac Nally, R.C., & J.M. Doolan, 1986b. An empirical approach to guild structure: habitat relationships in nine species of eastern-Australian cicadas. *Oikos* 47: 33–46.
- Mamet, J.R., 1957. A revised and annotated list of the Hemiptera (Heteroptera and Homoptera, excluding Sternorhyncha) of Mauritius. *Mauritius Institute Bulletin* 5(2): 31–81. [Cicadas 73, 74]
- McAlpine, D.K., 1977. Cicadas. In *The Australian Encyclopaedia*. 3rd edition. Grolier Society of Australia, Sydney. 2: 24–25. [Reprinted 1983, 4th edition, 2: 242–243]
- McKeown, K.C., 1942. Australian Insects. An Introductory Handbook. Royal Zoological Society of New South Wales, Sydney. 304 pp. [Second edition, 1944]
- McKeown, K.C., 1944. Australian insects. XX. Hemiptera-Homoptera. The cicadas. (Continued). *Australian Museum Magazine* 8: 234–237.
- McKeown, K.C., 1958. Cicadas. In: *The Australian Encyclopedia*. Second edition. Pp. 379–380.
- Melichar, Leopold, 1904. Neue Homopteren aus Süd-Schoa, Galla und den Somal-Ländern. Verhandlungen der Zoologisch-Botanischen Gessellschaft in Wien 54: 25–48.
- Metcalf, Z.P., 1963. General Catalogue of the Homoptera. Fasc.
  8. Cicadoidea. Part 1: Cicadidae. vii, 919 pages. Part 2,
  Tibicinidae: vi, 492 pp. [Species index by Virginia Wade, 1964, 26 pp] University of North Carolina State College, Raleigh, U.S.A.

- Michelsen, A., & H. Nocke, 1974. Biophysical aspects of sound communication in insects. Advances in Insect Physiology 10: 247–296
- Moss, J., 1997. Eprapah Creek field day—Saturday 9th November 1996. Butterfly and other Invertebrates Club Newsletter 5: 9–10.
- Moulds, M.S., 1983. Summertime is cicada time. *Australian Natural History* 20(12): 429–435.
- Moulds, M.S., 1985. *Illyria*, a new genus for Australian cicadas currently placed in *Cicada* L. (= *Tettigia* Amyot) (Homoptera: Cicadidae). *General and Applied Entomology* 17: 25–35.
- Moulds, M.S., 1986. *Marteena*, a new genus for the cicada *Tibicen rubricinctus* Goding and Froggatt (Homoptera: Tibicinidae). *General and Applied Entomology* 18: 39–42.
- Moulds, M.S., 1990. *Australian cicadas*. New South Wales University Press, Kensington. 217 pp., 24 col. pls.
- Moulds, M.S. (in prep). A review of the genera of Australian cicadas (Hemiptera: Cicadoidea).
- Moulds, M.S., & M. Carver, 1991. Superfamily Cicadoidea. In *The insects of Australia. A textbook for students and research workers*. Second Edition. Vol. 1, pp. 465–467. Melbourne University Press, Carlton.
- Musgrave, A., 1953. Seasonal occurrence of cicadas. *Australian Museum Magazine* 11: 10–15.
- Neave, S.A., 1939. Nomenclator Zoologicus. A List of the Names of Genera and Subgenera in Zoology From the Tenth Edition of Linnaeus 1758 to the End of 1935. Zoological Society of London, Regent's Park. 1: v-xiv, 1-957.
- Nixon, K.C., 1992. *Clados Reference*. *Version 1.1*. 39 pp. Privately published by the author.
- Noyce, J., 1980. Real dishy. *Queensland Naturalists Club News* 120: 9.
- Orian, A.J.E., 1954. A synopsis of the Cicadidae of Mauritius, with a description of *Mauricia claudeae*, gen. et sp. n. *Annals and Magazine of Natural History* (12)7: 233–237, pl. V.
- Orian, A.J.E., 1956. Hemiptera (Heteroptera and Homoptera excluding Sternorhyncha) of Mauritius. *Annals and Magazine of Natural History* (12)9: 641–654.
- Orian, A.J.E., 1964. The morphology of the male genitalia of *Abricta ferruginosa* (Stål) (Homoptera: Cicadidae). *Proceedings of the Royal Entomological Society of London* (A)39(1–3): 1–4.
- Popov, A.V., 1975a. The structure of the tymbals and the characteristics of the sound signals in singing cicadas (Homoptera, Cicadidae) in the southern regions of the USSR. *Entomological Review, Washington* 54(2): 7–35. [A translation of Popov, 1975b]
- Popov, A.V., 1975b. The structure of the tymbals and characteristics of sound signals of singing cicadas (Homoptera, Cicadidae) from the southern regions of the USSR. *Entomologicheskoe Obozrnie* 54(2): 258–290.
- Richards, O.W., & R.G. Davies, 1977. *Imms' General Textbook of Entomology*. 10th edition. Chapman & Hall, London. Vol.1, Structure, physiology and development: i–viii, 1–418 (cicadas pp. 183–185, fig. 9). Vol.2, Classification and biology: i–viii, 419–1354 (cicadas pp. 680–690, 709–711, figs. 316, 320, 330, 331).
- Schulze, F.E., W. Kükenthal, & K. Heider, 1926–1932. Nomenclator animalium generum et subgenerum. Im Auftrage der Preussischen Akademie der Wissenschaften zu Berlin. 5 vols. Im Verlage der Preussischen Akademie der Wissenschaften, Berlin. Pp. I–CCCXLIV, 1–3692. [Alphabetical list of genera; Abricta, 1926, 1: 4]
- Simmons, P., & D. Young, 1978. The tymbal mechanism and song patterns of the bladder cicada *Cystosoma saundersii*. *Journal of Experimental Biology* 76: 27–46.
- Singh-Pruthi, H., 1925. The morphology of the male genitalia in Rhynchota. *Transactions of the Royal Entomological Society of London* 1925: 127–267, pls. VI–XXXII.

- Stål, C., 1859. Hemiptera. Species novas descripsit. In Kongliga svenska Fregatten Eugenies resa omkring jorden under befäl af C. A. Virgin åren 1851–1853. Vetenskapliga iakttagelser På H. M. Konung Oscar den Förstes befallning utgifna af K. Svenska Vetenskaps Akademien. Zoologi 4: Pp. 219–298, pls. 3–4. Norstedt & Söner, Stockholm. [Cicadas pp. 269–270]
- Stål, C., 1861. Genera nonnulla nova Cicadinorum. *Annales de la Société entomologique de France* (4)1: 613–622.
- Stål, C., 1866. *Hemiptera Africana*. *Hemiptera Homoptera Latr*. Vol. 4, 276 pp, 1 pl. Officina Norstedtiana, Holmiae.
- Stål, C., [1870]. Hemiptera Fabriciana. Fabricianska Hemipterarter efter de i Köpenhamn och Kiel förvarade typexemplaren granskade och beskrifne. 2. Handlingar Kongliga Svenska Vetenskaps Akademiens, Stockholm 8(1): 1–130. [Title page dated 1869 but this issue not published until 1870.]
- Stevens, M.M., & M. Carver, 1986. Type-specimens of Hemiptera (Insecta) transferred from the Macleay Museum, University of Sydney, to the Australian National Insect Collection, Canberra. Proceedings of the Linnean Society of New South Wales 108(4): 263–266
- Swofford, D.L., 2000. PAUP\*. Phylogenetic Analysis Using Parsimony (\* and other methods). Version 4b10. Sinauer Associates, Sunderland, Massachusetts.
- Tillyard, R.J., 1926. *The Insects of Australia and New Zealand*. Angus & Robertson, Sydney. 560 pp, 44 pls.
- Wagner, W., 1968. Cicadina. In Die entomologischen Sammlungen des Zoologischen Staatsinstituts und Zoologischen Museums Hamburg. VII Teil, Insecta IV, H. Weidner & W. Wagner. Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut 65: 134–156.
- Walker, F., 1850. List of the Specimens of Homopterous Insects in the Collection of the British Museum. Part 1. British Museum, London. 1–260.

- Wilson, P., 1970. *Australia's Insect Life*. Horwitz, North Sydney. 50 pp., illustr.
- Woodward, T.E., J.W. Evans & V.F. Eastop, 1970. Hemiptera (Bugs, Leafhoppers, etc.). In *The Insects of Australia*, chapter 26. Melbourne University Press. Pp. 387–457, pl. 3. [Cicadas pp. 410–413; pl. 3, fig. G].
- Young, D., 1972a. Neuromuscular mechanism of sound production in Australian cicadas. *Journal of Comparative Physiology* 79: 343–362.
- Young, D., 1972b. Analysis of songs of some Australian cicadas (Homoptera: Cicadidae). *Journal of the Australian Entomological Society* 11(3): 237–243.
- Young, D., 1973. Sound production in cicadas. *Australian Natural History* 17(11): 375–380.
- Young, D., & R.K. Josephson, 1983a. Mechanisms of soundproduction and muscle contraction kinetics in cicadas. *Journal* of Comparative Physiology 152: 183–195.
- Young, D., & R.K. Josephson, 1983b. Pure-tone songs in cicadas with special reference to the genus *Magicicada*. *Journal of Comparative Physiology* 152: 197–207.
- Zborowski, P., & R. Storey, 1995. A Field Guide to Insects in Australia. Reed Books, Chatswood. 207 pp., illustr.
- Zimsen, E., 1964. *The Type Material of I. C. Fabricius*. Munksgaard, Copenhagen. 656 pp.

Manuscript received 26 April 2001, revised 7 November 2002 and accepted 20 November 2002.

Associate Editor: D.J. Bickel.

#### Index

Abricta 254, 257	Tryella crassa n.sp	283
Abricta brunnea	Tryella graminea n.sp	
Abricta ferruginosa260	Tryella infuscata n.sp	
Chrysolasia n.gen	Tryella kauma n.sp	
Chrysolasia guatemalena, n.comb 262	Tryella lachlani n.sp	
Aleeta n.gen	Tryella noctua, n.comb	
Aleeta curvicosta, n.comb	Tryella occidens n.sp	
<i>Tryella</i> n.gen	Tryella ochra n.sp	
Tryella adela n.sp	Tryella rubra, n.comb	295
Tryella burnsi n.sp	Tryella stalkeri, n.comb	
Tryella castanea, n.comb	Tryella willsi, n.comb	298

# Dendroid and Tuboid Graptolites from the Llandovery (Silurian) of the Four Mile Creek Area, New South Wales

R.B. RICKARDS<sup>1</sup>, A.J. CHAPMAN<sup>1</sup>, A.J. WRIGHT<sup>2\*</sup> AND G.H PACKHAM<sup>3</sup>

<sup>1</sup> Department of Earth Sciences, University of Cambridge, Cambridge CB2 3EQ England wagreen@esc.cam.ac.uk

<sup>2</sup> School of Geosciences, University of Wollongong, Wollongong NSW 2522, Australia tony\_wright@uow.edu.au

<sup>3</sup> School of Geosciences, University of Sydney NSW 2006, Australia gpackham@mail.usyd.edu.au

ABSTRACT. Twenty-four taxa of Llandovery (Early Silurian) dendroid and tuboid graptolites from the Cadia Coach Shale and Glendalough Formation in the Four Mile Creek area, S of Orange, New South Wales, provide the most diverse benthic graptolite record known from rocks of this age.

Eighteen new taxa described here are: the dendroids *Dendrograptus avonleaensis*, *D. ashburniaensis*, *Dictyonema williamsae*, *D. paululum australis*, *D. jenkinsi*, *D. muirae*, *D. warrisi*, *Callograptus bridgecreekensis*, *C. rigbyae*, *C. ulahensis*, *Stelechocladia praeattenuata*, *Acanthograptus praedeckeri*, *A. praedeckeri minimus*, *Thallograptus christoffersonae*, *Koremagraptus obscurus* and *C. elegantulus*; and the tuboids *Reticulograptus thomasi* and *Cyclograptus*? *australis*. The six previously-named taxa are: *Dictyonema* cf. *delicatulum* Lapworth, *D. falciferum* Bulman, *D. venustum* Lapworth, *Callograptus* cf. *niagarensis* Spencer and *Pseudodictyonema graptolithorum* (Počta); and one species in open nomenclature is *Dictyonema* sp. 1. These occur with graptoloids at Four Mile Creek, allowing precise stratigraphic correlation of the faunas with probably the *gregarius* Biozone (middle Llandovery), and the *crispus* and *griestoniensis* Biozones (late Llandovery) of Europe.

Criteria for dendroid classification are discussed and some implications for reconstructing the evolutionary history of the group are reviewed. The evolution of anastomosis and dissepiments is seen as of prime importance in the development of three major changes in the Middle to Late Cambrian, which are: 1, ordered  $Dendrograptus \rightarrow Callograptus$ : 2, ordered  $Dendrograptus \rightarrow Dictyonema$ ; 3. ordered  $Dendrograptus \rightarrow Desmograptus$ . The development of compound stipes, while important in defining the Acanthograptidae, is recognized as having arisen independently in three other lineages.

RICKARDS, R.B., A.J. CHAPMAN, A.J. WRIGHT & G.H PACKHAM, 2003. Dendroid and tuboid graptolites from the Llandovery (Silurian) of the Four Mile Creek area, New South Wales. *Records of the Australian Museum* 55(3): 305–330.

#### **Contents**

Geological setting	307
Classification of dendroid graptolites	
Dictyonema J. Hall, 1851 and Callograptus J. Hall, 1865	
Acanthograptus Spencer, 1878 and Thallograptus Ruedemann, 1925	
Dendroid bithecal morphology	
Dendroid autothecal apertural variation	312
Systematic palaeontology	
Order Dendroidea Nicholson, 1872	312
Family Dendrograptidae Roemer, in Frech, 1897	
Genus Dendrograptus J. Hall, 1858	
Dendrograptus avonleaensis n.sp.	
Dendrograptus ashburniaensis n.sp.	
Genus Dictyonema J. Hall, 1851	
Dictyonema cf. delicatulum Lapworth, 1881	
Dictyonema williamsae n.sp.	
Dictyonema falciferum Bulman, 1928	
Dictyonema venustum Lapworth, 1881	
Dictyonema paululum australis n.subsp.	
Dictyonema jenkinsi n.sp.	
Dictyonema muirae n.sp.	
Dictyonema warrisi n.sp.	
Dictyonema sp. 1	
Callograptus bridgecreekensis n.sp	
Callograptus ulahensis n.sp	
Callograptus cf. niagarensis Spencer, 1878	
Family Pseudodictyonemiidae Chapman <i>et al.</i> , 1993	
Genus Pseudodictyonema Bouček, 1957	
Pseudodictyonema graptolithorum (Počta, 1894)	
Family Stelechocladiidae Chapman <i>et al.</i> , 1993	
Genus Stelechocladia Počta 1894	
Stelechocladia praeattenuata n.sp	
Family Acanthograptidae Bulman, 1938	
Genus Acanthograptus Spencer, 1878	
Acanthograptus praedeckeri praedeckeri n.sp.	
Acanthograptus praedeckeri minimus n.subsp.	
Genus Thallograptus Ruedemann, 1925	
Thallograptus christoffersonae n.sp.	
Genus Koremagraptus Bulman, 1927	
Koremagraptus obscurus n.sp.	
Koremagraptus elegantulus n.sp.	327
Order Tuboidea Kozlowski, 1938	328
Family Tubidendridae Kozlowski, 1938	328
Genus Reticulograptus Wiman, 1901	328
Reticulograptus thomasi n.sp.	328
Family Idiotubidae Kozlowski, 1949	328
Genus Cyclograptus Spencer, 1884	328
Cyclograptus? australis n.sp.	328

Silurian graptolite faunas have been known from the Four Mile Creek (formerly known as Panuara Rivulet) area (Fig. 1) S of Orange (33°17'S 149°6'E), New South Wales, for 50 years (Stevens & Packham, 1953). These fossils are important in the global context as they give a basis for very fine correlation of Silurian strata; when these NSW faunas are fully documented, they will provide a framework for calibration of the geological evolution of this part of the eastern Lachlan Fold Belt. This is potentially important in view of the active gold exploration programmes in the region (see also Packham *et al.*, 1999). In

the global context, these studies will shed more light on the evolution, palaeoecology and biogeography of graptolites. In addition, far-reaching tectonic and sea level interpretations (Jenkins, 1978; Packham, 1969) have been made on the basis of preliminary identifications of the faunas, and some of these interpretations have been quoted in global considerations of Silurian sea level changes (Johnson *et al.*, 1991; Johnson & McKerrow, 1991); there is an urgent need to describe and assess the present faunas fully to permit evaluation of these interpretations.

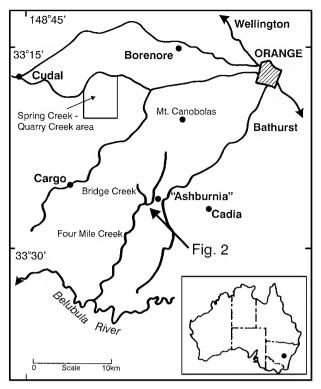


Fig. 1. Location map of the Bridge Creek area of southeastern Australia.

#### Previous studies of the area

Pioneering studies in the southern part of the area by Booker (1950) recognized a belt of limestone extending from the Belubula River in the S to Cobblers Creek in the N; Booker considered this Late Silurian, which is not supported by later studies. Carne & Jones (1919: 177–178) mentioned that limestone extended from (what is now known to be Ordovician) Cliefden Caves across the Belubula River into portion 3, parish Carlton, county Bathurst. Stevens & Packham (1953) greatly extended knowledge of the Ordovician and Silurian strata in the region and first interpreted the graptolite faunas of the area. Detailed mapping and palaeontological studies of the Four Mile Creek region were carried out by Warris (1964) and Jenkins (1973).

Graptolites previously described and illustrated from the Four Mile Creek area include the Llandovery species Glyptograptus tamariscus, Monograptus triangulatus,

Monograptus intermedius and Rastrites longispinus described by Sherrard (1954: pl. XI, 99–100) and the Wenlock fauna described by Rickards & Wright (1997). Sherrard (1954: 90–91) listed several Llandovery faunas and one Wenlock graptolite fauna from the "Angullong" area S of the Bridge Creek area, and illustrated Cyrtograptus cf. insectus (Sherrard, 1954: 76, fig. 1.3) and Monograptus exiguus, M. marri and M. dubius (Sherrard, 1954, figs. 1.1, 1.4, and 1.5 respectively) from "Four Mile Creek". Apart from these very preliminary studies of the faunas, there remain rich and essentially undescribed Llandovery, Wenlock and Ludlow graptolite faunas in the area.

In addition to the prolific, diverse and well-preserved graptolites of the Llandovery to Ludlow of the Four Mile Creek area, important faunas are known elsewhere in the region from Spring and Quarry Creeks (Packham & Stevens, 1955; Rickards *et al.*, 1995), and from Cheesemans Creek (Sherwin, 1971); both areas are located N of the present study area (Fig. 1).

This paper is the first part of our investigation and interpretation of the Four Mile Creek faunas, biostratigraphy and sequences. We describe here by far the most diverse Llandovery dendroid graptolite fauna on record, being almost exclusively from several localities in the valley of Bridge Creek, a major tributary of Four Mile Creek (Figs. 1, 2).

# Geological setting

Silurian strata discussed here occur south and west of the old settlement of Four Mile Creek in the gently undulating topography of the valley of Four Mile Creek; the most important outcrops are in or along Four Mile Creek, its tributaries Bulls Camp Creek and Bridge Creek, and (a tributary of the latter) Wallace Creek (Fig. 2). Silurian faunas have also been documented from strata east of Four Mile Creek in the vicinity of the Cadia Mine, in an area of predominantly Ordovician rocks (Offenberg, 1963; Rickards *et al.*, 2001).

The faunas described here are from the two lower groups of the three comprising the Silurian to basal Devonian succession in the Four Mile Creek area; these are, in ascending order, the Ashburnia, Waugoola and Mumbil Groups (Pogson & Watkins, 1998). Our collections are from strata exposed on the eastern limb of a syncline (Fig. 2); the west-dipping succession has been disrupted by faulting and is uncleaved; Cthe graptolite faunas are largely undeformed. In this area the Ashburnia and Waugoola

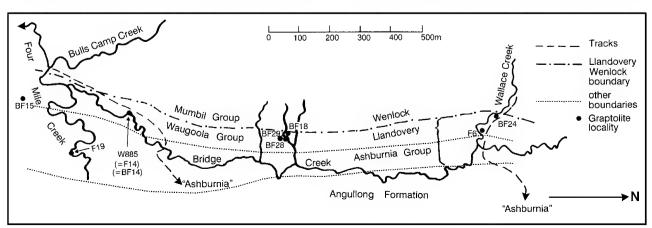


Fig. 2. Dendroid graptolite localities on the Bridge Creek sections.

**Table 1.** Lithostratigraphic units from the Four Mile Creek area, according to current terminology, which are mentioned in text; all named units are not shown. New faunal data and mapping indicate a hiatus above the *spiralis* bed, and the Burly Jacky Sandstone is placed in the Mumbil Group. Units that have yielded graptolites are in bold type.

MUMBIL GROUP	Wallace Shale	
(Wenlock-Pridoli)	Ulah Formation	higher beds Burly Jacky Sandstone Member
WAUGOOLA GROUP (late Llandovery)  Glendalough	Glendalough Formation	spiralis beds (griestoniensis Biozone)
	Giendalough Formation	exiguus bed (crispus Biozone)
ASHBURNIA GROUP (early to middle Llandovery)	Cadia Coach Shale	Avon Lea Mudstone Member (gregarius Biozone)
	Bagdad Formation	

Groups are about 80 and 60 m thick respectively, consisting of calcareous and clastic sediments. There is an erosional break or unconformity between the Ashburnia Group and the underlying Late Ordovician volcanic Angullong Formation. The Silurian strata are overlain unconformably by gently folded Late Devonian sandstone, conglomerate and shale forming timbered ridges almost exclusively located on the W side of Four Mile Creek.

The Silurian lithostratigraphic sequence in the area has been described in detail by Jenkins (1973, 1978, 1986) and Pogson & Watkins (1998), and is summarized in Table 1. From our preliminary reassessment of the faunas and field studies (both here and at Spring-Quarry Creek: see Fig. 1) it seems likely that changes will be necessary to the stratigraphic terminology and relationships, and age assignments. For instance, our studies indicate that the Burly Jacky Sandstone Member and overlying strata placed by Jenkins (1978) in the Waugoola Group should be recognized as part of the Mumbil Group (Table 1). Nevertheless, the stratigraphic position of the present faunas from in the immediate vicinity of Bridge Creek (Fig. 2) is very clear and, based on our preliminary study of the associated graptoloids, we agree broadly with age assignments made for these dendroid faunas by Jenkins (1978).

The oldest Silurian unit in the area is the early to middle Llandovery Ashburnia Group, a name introduced by Pogson & Watkins (1998) to replace the Cadia Group of Jenkins (1978). The basal Bagdad Formation of clastics and limestones, which includes the Bridge Creek Limestone Member, is overlain by the Cadia Coach Shale. At the base of the latter formation is the Avon Lea Mudstone Member; locality F19 is located in this unit, and is provisionally assigned by us to the uppermost *gregarius* Biozone of middle Llandovery age. The only dendroid species from this locality is *Stelechocladia praeattenuata* n.sp., also known from higher localities. All other localities discussed herein are from the overlying Waugoola Group.

The late Llandovery Waugoola Group is represented in the area in Fig. 2 by the Glendalough Formation. Jenkins (1978, 1986) divided the lower shaly part of the formation into two units; siliceous sandy shale in the lower part which he termed the "exiguus bed" and the upper olive green shaly unit which he called the "spiralis beds". Localities BF15 and F6 in the "exiguus bed" are within the crispus Biozone (of late Llandovery age). In the lower part of the "spiralis beds", locality BF14 (= W885 and F14) is in the lower part of the griestoniensis Biozone and localities BF 28, BF 29, BF24 and BF18 are from the upper part of the "spiralis beds" and have been correlated with the upper griestoniensis Biozone (also of late Llandovery age). The last mentioned locality (BF18) is in the highest beds of the "spiralis beds" where the shales are more siliceous and thin bands of lithic sandstone are interbedded; Stomatograptus grandis is also present at this level.

#### Faunal assemblages

The faunas discussed here have been collected from eight localities, one of which (F14=BF14=W885) has produced by far the largest assemblage of 18 species (Table 2). At this locality dendroids outnumber graptoloids in both diversity and abundance. F19 is located within the Avon Lea Mudstone Member of the Cadia Coach Shale, Ashburnia Group; and all other localities are in the Ashburnia Group.

# Comparison with other late Llandovery dendroid faunas

The late Llandovery has in many parts of the world wellpreserved dendroid graptolite faunas, but none has the high diversity recognized at Four Mile Creek. Bulman's (1928) monograph on British dendroids, for example, listed only five species for the whole of Britain, and Bull (1987) recorded six species from rich and well-preserved dendroid faunas in the late Llandovery of Scotland. In his classic monograph on Czech dendroids, Bouček (1957) recorded only 6 species from the whole Llandovery; although this work has been supplemented by further records of a small number of species by Kraft (1979, 1984), only a few are from the late Llandovery. Ruedemann (1947) recorded over 70 dendroid taxa for the Silurian of North America, but proportionally fewer from the late Llandovery, and most of these are in low diversity assemblages. The most spectacularly diverse North American dendroid faunas are from the Lockport

**Table 2.** Stratigraphic distribution of dendroid graptolite taxa described in this paper (closed circle = presence). The oldest locality F19 (Avon Lea Mudstone Member, Cadia Coach Shale, Ashburnia Group) is at extreme left. All other, younger localities (Glendalough Formation, Waugoola Group) range from the lowest locality BF15 at the left, to the youngest locality BF18 at extreme right.

	F19	BF15	F6	F14	BF28	BF29	BF24	BF18
Dendrograptus avonleaensis n.sp.	0	0	0	•	0	0	0	0
Dendrograptus ashburniaensis n.sp.	0	0	0	•	0	0	0	0
Dictyonema jenkinsi n.sp.	0	0	0	•	0	0	0	0
Dictyonema muirae n.sp.	0	0	0	•	0	0	0	0
Dictyonema venustum	0	0	0			0	0	0
Dictyonema sp. 1	0	0	0	•	0	0	0	0
Dictyonema falciferum	0	0	0	•	0	0	0	0
Dictyonema cf. delicatulum	0	0	0		0	0	0	0
Dictyonema paululum australis n.sp.	0	0	0	•	0	0	0	0
Dictyonema williamsae n.sp.	0	0	0	•	0	0	0	0
Dictyonema warrisi n.sp.	0	0	0	•	0	0	0	0
Callograptus rigbyae n.sp.	0	0	$\circ$	•	•	0	0	0
Callograptus bridgecreekensis n.sp.	0	0	0	•	0	0	0	0
Callograptus cf. niagarensis	0	0	0	•	0	0	0	0
Callograptus ulahensis n.sp.	0	•	$\circ$	0	0	0	0	0
Pseudodictyonema graptolithorum	0	0	0	•	0	0	0	0
Stelechocladia praeattenuata n.sp.	•	0	0	0	•	0		•
Acanthograptus praedeckeri n.sp.	0	0		•	•	•	0	0
Acanthograptus p. minimus n.subsp.	0	0	•	0	0	0	0	0
Thallograptus christoffersonae n.sp.	0	0	0	•	•	•	0	0
Koremagraptus obscurus n.sp.	0	0	0	0	•	0	0	0
Koremagraptus elegantulus n.sp.	0	0	0	•	0	0	0	0
Reticulograptus thomasi n.sp.	0	0	0	0	•	0	0	0
Cyclograptus? australis n.sp.	$\circ$	0	0	0	•	0	0	0

dolomites and limestone (Ruedemann 1947, pp. 128–9) but these are of Wenlock/Ludlow age. Silurian dendroids are known from both Russia and China but no Llandovery horizons have been described with highly diverse dendroid faunas: for example Obut & Sobolevskaya (1966) recorded three dendroid species from the early Llandovery (and one species from the early Wenlock).

#### Preservation of the graptolites

There is no tectonic deformation of the graptolites. There is some crumpling of stipes during burial and diagenetic flattening, but this is usually infrequent and easily detected. A surprising number of specimens are more or less complete, some with holdfasts, or are large fragments, indicating that transport has been low: however, dendroid debris indicates that some transport has occurred so that the assemblages cannot be considered as biocoenoses. The rock type is mud to silt grade with occasional fine sand laminae, and some hemipelagic layers. In general the stipes are in low relief, the original (carbonized) periderm well-preserved, and there may be partial infills of mud or pyrites. Specimens in full relief, or fully infilled with pyrites have not been observed.

#### Classification of dendroid graptolites

The most recent attempt to arrange dendroids in a provisional classification was by Chapman *et al.* (1996). They noted that rhabdosomal form seemed of lesser importance in classification than the manner in which the stipes were connected, so that species of *Dictyonema* might be conical, cyathiform, or discoidal. However, the uniting

feature of species of *Dictyonema* is the branching pattern and the stipe connections by numerous dissepiments. *Callograptus* can be conical or flabellate, is very similar, but has few or no dissepiments. In *Desmograptus* Hopkinson *in* Hopkinson & Lapworth, 1875, the stipes unite by anastomosis, as they do in *Polygonograptus* Bouček, 1957, but the bulk of the remaining genera exhibit *Dendrograptus* style of bushy branching (see Chapman *et al.*, 1996, figs. 2, 3). Some genera such as *Koremagraptus* exhibit a variety of stipe connections usually involving autothecal transfer from one stipe to another.

Stipe structure has some broad classificatory value in that the Acanthograptidae develop compound stipes, whereas most of the Dendrograptidae have relatively simple stipes. However, in the Dendrograptidae, *Callograptus* gave rise to the compound *Pseudocallograptus* Skevington, 1963, *Dictyonema* gave rise to *Pseudodictyonema* Bouček, 1957, and *Dendrograptus* gave rise to *Stelechocladia* Počta, 1894.

These classificatory features were placed in a stratigraphic context by Chapman *et al.* (1996; see Figs. 2, 3 herein). Thus the bushy dendroid habit is the earliest in the stratigraphic record, followed quickly by more regular branching patterns, then stipe connections through anastomosis and dissepiments, and the development of conical and other more ordered colonies (*Callograptus, Dictyonema* and *Desmograptus*).

Chapman et al. (1996) concluded that there was a morphological and stratigraphic series, beginning in the Middle Cambrian, from *Dendrograptus* (disordered and ordered) to *Callograptus*, *Dictyonema* and *Desmograptus*,

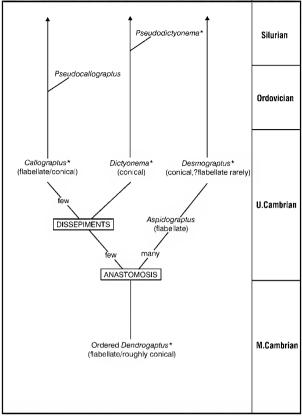


Fig. 3. Early evolution of some benthic Dendroidea, and modifying the suggestions of Chapman *et al.* (1996), and illustrating the rôle of anastomosis and dissepiments development. Full explanation is to be found in text. Asterisks indicate genera from which species are described in this paper. Boxes indicate approximate time of appearance of that character.

and that this supported the use of rhabdosomal stipe connection (but not gross geometry) in classification. Some questions were raised, however, as in the cases of *Dictyonema* v. *Callograptus*, *Acanthograptus* v. *Thallograptus*, and in the use of simple stipes v. compound stipes. These questions are discussed further below, but the basic classification used here is that of Chapman *et al.* (1996). In our opinion the present level of knowledge of dendroid morphology is inadequate for meaningful cladistic analysis.

# Dictyonema J. Hall, 1851 and Callograptus J. Hall, 1865

The distinctions between these two genera are not very great. Bulman (1970) considered *Callograptus* to have no dissepiments or to have fewer than *Dictyonema*. Both genera originate in the Middle Cambrian (see Chapman *et al.*, 1996, fig. 2) and range into the Carboniferous. Both genera have rhabdosomes with varying geometry, although each species seems to have a single mode of growth. Both genera have regular branching patterns, and long parallel stipes: and they both exhibit the same range of variations of autothecal and bithecal type. The sole difference seems to be the extent to which dissepiments are developed: *Callograptus* has none or few; *Dictyonema* has common dissepiments. Species of *Callograptus* with no dissepiments are not unlike some of the earliest species of *Dendrograptus* (see Chapman *et al.*, 1996, p. 195) which have fairly ordered

branching patterns and long, roughly parallel stipes in bushy, flabellate and possibly conical rhabdosomes. However, in *Dendrograptus* the autothecae remained simple denticulate whereas in *Callograptus* quite varied autothecae were quickly evolved.

The evolutionary scenario deduced by Chapman et al. (1996) was of ordered Dendrograptus species giving rise in the Middle Cambrian to Callograptus and Dictyonema by increased development of dissepimental connecting bars between adjacent stipes, with a concomitant restriction in the arrangement of stipes giving rise to flabellate and conical rhabdosomes. In the present work, Fig. 3 extends and revises the relationships deduced in the earlier paper, suggesting that the development of anastomosis and dissepiments were key stages in the evolution of the benthic Dendroidea. This reinforces the earlier suggestion that the method of stipe connection is of more significance taxonomically than is rhabdosome morphology.

# Acanthograptus Spencer, 1878 and Thallograptus Ruedemann, 1925

The working distinctions between the two genera seem to be that *Acanthograptus* has short twig-like processes developed ventrolaterally from the main stipes, and placed alternatively along the stipe: each twig comprises several thecal tubes, most usually two autothecae (with two bithecae opening near the base of the twig). *Thallograptus*, on the other hand, has stipes and twigs which gradually become thinner as autothecae "peel off" to open as individual tubes projecting either from the sides of the stipe (and, therefore, are superficially twig-like) or projecting ventrally. In both genera the rhabdosomes are usually dendroid and both have compound stipes.

However, the type species Acanthograptus granti Spencer, 1878, is less regular than the above generally held concept, although it undoubtedly has twigs amongst a dense branching pattern. Similarly A. praedeckeri n.sp. of this paper has a very frequent branching pattern (yet between branches has conspicuous twigs alternating along the stipe) and the stipes are clearly compound. In A. impar and A. murciformis, both described by Bulman & Rickards (1966), the stipes are compound and a fairly regular sequence of autothecae is maintained. In these species, however, a breakdown of regularity is apparent: not all twigs show the 2+2 pattern, and many autothecae and bithecae open adventitiously, with some autothecae opening erect and isolated—an incipient *Thallograptus* pattern. It would seem that there is a morphological continuum from the simplest of acanthograptids through the most complex, with compound stipes and breakdown of the twig structure, to thallograptids. However, individual evolutionary lineages have not been worked out; although one can conclude that because thallograptids are more common in the Silurian than acanthograptids, (the reverse being true in the Ordovician), then thallograptids probably evolved from acanthograptids. One can predict, therefore, that lineages of increasing stipe complexity may eventually be recognized. For the present most species fall fairly readily into the two genera, but in the present paper Acanthograptus praedeckeri n.sp. and Thallograptus christoffersonae n.sp. are not easy to distinguish because their rhabdosomes are so similar.

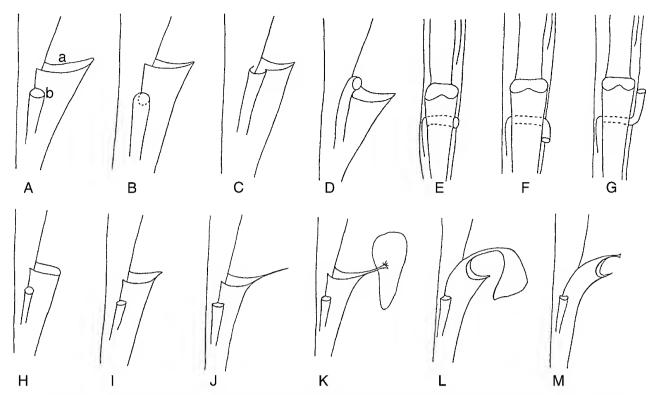


Fig. 4. A-G, different types of bithecae: A, Bulman's (1928, 1933) Type 1 with bitheca n+1 opening along the lateral wall of autotheca n. This is the most common of autothecal/bithecal relationships; B, C, Bulman's (1928, 1933) Type 2 in which the bithecal aperture opens inside the autothecal tube or aperture; D, Bulman's (1928, 1933) Type 3 where the n+1 bithecal aperture is located on the dorsal side of the aperture of autotheca n; E, Bulman's (1928, 1933) Type 4 in which the bithecal tube n+1 passes between the dorsal wall of autotheca n and the ventral wall of autotheca n+1; F, G, Bulman's (1928, 1933) Type 5 a modification of Type 4 in which the bithecal tube turns proximally or distally before the bithecal aperture is reached; E, autothecal variation in E E0 and E1 in which the projects as a spine which may or may not bifurcate; E1, the ventral process is adorned with a large shield-like plate; E2, the dorsal apertural process has plate-like process hanging more or less in front of the aperture; E1 bithecal arrangement is shown; fuselli omitted; E1, autothecal aperture; E2, bithecal aperture; these structures are described or commented upon in various places in the text.

# Simple stipes and compound stipes

The question of compound stipes raises problems elsewhere in the dendroid classification. For example Chapman et al. (1996) placed *Pseudodictvonema*, with its compound stipes, in a new family, the Pseudodictyonemiidae, which ranges from the Silurian to the Carboniferous. However, some care must be taken: many stipes of species of Dictyonema appear superficially to have complex stipe structure because all dendroid thecae are narrow and elongate and in dorsal view a ropy texture may be apparent in well preserved specimens. The complexity has to be such that there is a clear indication of more than one line of stolonal development in any one cross section of the stipe (see, for example, Bulman & Rickards, 1966, figs. 20-23). In this work Pseudodictyonema graptolithorum (Počta) is such a case. We suspect that many more species will prove to have compound stipes when suitably preserved material is obtained. Indeed, compound stipes have evolved in a number of lineages, and Chapman et al. (1996) recognized four separate origins for this condition.

#### Dendroid bithecal morphology

Most dendroid species have bithecae comprising small, inconspicuous tubes, with unornamented apertures, which open inconspicuously on the lateral or, occasionally, other

parts of the stipe wall. Some open inside the autothecal apertural region. There are, however, more unusual types of bithecae. These were first summarized by Bulman (1927–1967) and he later (1933) gave a more detailed classification of them, defining five types (Fig. 4): Type 1 consisting of the simpler form described above, opening externally just below or level with the autothecal aperture; Type 2 being those forms which open into the autothecal apertural region; Type 3 embracing all forms which open between the apertural region of autotheca n and the early free ventral wall of autotheca n+1; Type 4 which grows beyond the point of Type 3 and opens facing laterally; and Type 5 being a morphological step beyond Type 4 in which the bithecal apertural region curves proximally or distally.

The stratigraphy of these morphological types was investigated by Chapman & Rickards (1982) who concluded that the more complex types 4 and 5 (Fig. 4E–G herein) were stratigraphically younger, appearing respectively in the Caradoc and Ashgill series (Ordovician) and being fairly common in Silurian species.

However, even today bithecae are known in relatively few dendroid species and the situation may be more complex than depicted in Fig. 4. For example, Rickards *et al.* (2001) recorded an Iranian late Arenig species of *Dictyonema* in which the bithecae open as long narrow tubes in the spaces of the meshwork, and are isolated for

almost one millimetre of their length. Such a bithecal form does not fall into Bulman's (1933) classification of types, but could be a morphological extension of Types 1, 3, 4 or 5, but presumably not of Type 2.

Based on our present studies *Dictyonema muirae* n.sp. appears also to have aperturally isolated bithecae, but in this case they are conspicuous structures rather overshadowing and overhanging the autothecae (Fig. 13C). Such thecae could develop from the subtype of Type 5 where the bithecal tube curves distally (Fig. 4F,G). Rickards *et al.* (2001) described a comparable structure in their new species, *Callograptus huckriedei*, from the late Arenig of Iran.

These observations suggest that the broad evolution of dendroid bithecae suggested by Chapman & Rickards (1982) is oversimplified: bithecae may become more complicated through time, but Type 5 structures may have been present rather earlier than supposed.

#### Dendroid autothecal apertural variation

Possibly for reasons of serendipity most of the classic early work on well-preserved (and isolated) dendroids (e.g., Wiman, 1901; Bulman, 1927–1967, 1933; Kozlowski, 1938, 1949) has described species with relatively simple autothecal apertures. Specimens "in the rock" also suggest that most dendroid species have autothecal apertures with a short ventral denticle. Exceptions were described, such as Dictyonema peltatum Wiman, 1901 (see Bulman & Rickards, 1966) in which the ventral process develops a large shield-like plate, and in which adjacent plates may coalesce. Other species have the dorsal part of the aperture developed as a spine or process, as in Dictyonema rhinanthiforme Bulman, 1933 (see Chapman & Rickards, 1982 for detail). Dictyonema rhinanthiforme was originally recorded from the late Arenig or early Llanvirn of Sweden but the Chapman & Rickards (1982) material came from the early Llandovery of the Canadian Arctic region.

In some dendroids, especially *Dictyonema* and *Callograptus*, the autothecal apertures are slightly isolated from the main stipe. These forms may have a ventral denticle, a dorsal process, or both, as in the cases of *D. rhinanthiforme* and *D. elegans* Bulman, 1928 (see also Rickards & Wright, 1997, 1999).

The present collection has a species with isolated autothecal apertures, *D. williamsae* n.sp., although in this case there appear to be no apertural processes. On the other hand *D. warrisi* n.sp. has unusually long ventral apertural spines, a feature we have not seen recorded in dendroids before (except in *Dictyonema* sp. where the spines bifurcate; see Rickards *et al.*, 1995). Further discussion is given under the description of *D. warrisi* n.sp.

In one of the few works on NSW dendroids, Sherrard (1956, table 1) tabulated some characters of NSW Ordovician and Silurian forms assigned to *Dictyonema*, but did not describe any dendroids from the Four Mile Creek area. She described material from Silurian strata at Spring-Quarry Creek, including an indeterminate Llandovery *Dictyonema* sp. and the new (? Ludlow) species *Dictyonema favosum* and *Reticulograptus undulosum*. From the Ludlow of Yass she described ?*Dictyonema* sp. and the new species *Dictyonema vinculosum*, and noted that *D. favosum* was found with the graptolite from Yass that was then called *Monograptus bohemicus* (but see Rickards & Wright, 1999).

#### Systematic palaeontology

Material studied here has been collected by GHP over many years, by Dr Chris Jenkins and by RBR, AJW and GHP in 2000, with assistance from Dr Ian Percival and Ms Lucy Muir in 2000. Material described herein is deposited in the Australian Museum, Sydney and bears the prefix AM F. Localities prefixed by the letter W refer to collections made in November, 2000; those with the prefix F refer to collections made by Packham, and those with the prefix BF refer to collections made by Jenkins (1973). Although some of these localities are probably the same (e.g., W885, BF14 and F14) we have referred to them with their original prefixes or locality number in each case.

# Class Graptolithina Bronn, 1849 Order Dendroidea Nicholson, 1872 Family Dendrograptidae Roemer, *in* Frech, 1897 *Dendrograptus* J. Hall, 1858

**Type Species**. *Graptolithus hallianus* Prout, 1851; subsequently designated by J. Hall (1862).

# Dendrograptus avonleaensis n.sp.

Figs. 5A, 6A,B

Material. HOLOTYPE AM F114646a-b and PARATYPES AM F114650 and AM F114766, all from F14, Bridge Creek.

**Etymology**. After the property "Avon Lea" on which F14 is located.

**Diagnosis**. *Dendrograptus* with robust funnel-shaped rhabdosome at least 15 mm long and 18 mm at its widest; branching in broad zones; stipes with a dorsoventral width of 0.50–0.60 mm and a lateral width of 0.20–0.40 mm; autothecal spacing 18–20 in 10 mm.

Description. The holotype (Fig. 6B) displays a distal array of at least 48 stipes arranged in a broadly conical fashion with two major branching zones. These distal stipes diverge some 3.5 mm above the visible base of the specimen, but they do not arise from a solid stem: tightly clustered stipes are visible in the densely packed area. The overall shape is, therefore, funnel-shaped with a proximal constriction. In one or two places the stipes are visible in profile when the autothecae, spaced at 18–20 in 10 mm, can be seen to be of simple denticulate type (Fig. 4I). The lateral stipe width is 0.40 mm proximally, falling to 0.20 mm most distally, suggesting some cortical thickening as the colony ages. Two other specimens (e.g., Fig. 5A) are fragments from beyond the zone of expansion. They show some of the above-described features but less well-displayed.

Remarks. As described by Chapman et al. (1996) some Dendrograptus species can be quite well ordered; this is one such species, having a broadly conical, funnel-shaped form and rough branching zones. Dendrograptus avonleaensis n.sp. has a superficial resemblance to Calyptograptus cyathiformis Spencer, 1878 from the Niagara Limestone, but that species has more frequent and irregular branching and a robust stem; the thecae of C. cyathiformis are not known. Dendrograptus avonleaensis differs from D. ashburniaensis n.sp. herein in that the latter has a thecal

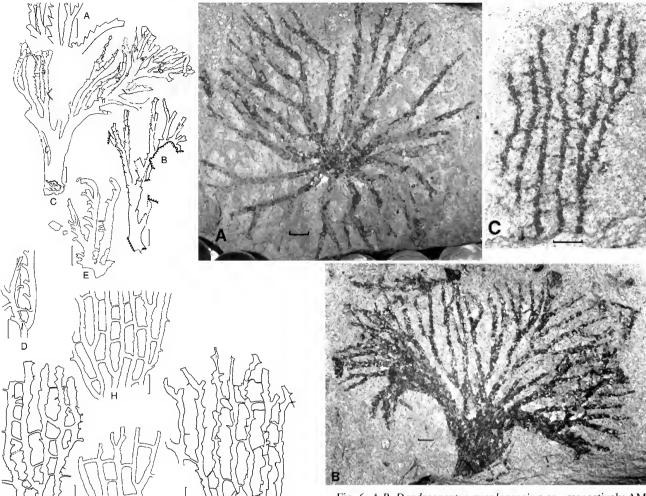


Fig. 5. A, Dendrograptus avonleaensis n.sp., holotype AM F114646b, BF14; B,C, Dendrograptus ashburniaensis n.sp., respectively AMF114566 and holotype 114567, both from F14; D-F, Dictyonema williamsae n.sp., respectively holotype AM F114565, AM F114758, part of basal holdfast present, and holotype AM F114565, showing dorsoventral view of stipes, all from W885; G, Dictyonema cf. delicatulum, AM F114648a, W885; H, Dictyonema venustum, AM F114048a, W885; I, Dictyonema falciferum, AM F114750, F14. Scale bars 1 mm; in B and C, hatched areas indicate that specimen is obscured by sediment.

spacing of 36 in 10 mm, almost twice that of the former; and *D. ashburniaensis* develops a thickened stem proximally.

#### Dendrograptus ashburniaensis n.sp.

Fig. 5B,C

**Material**. HOLOTYPE AM F114567 and PARATYPE AM F114566, both from F14, Bridge Creek.

**Etymology**. After the nearby property of "Ashburnia", at the former Four Mile Creek post office.

**Diagnosis.** *Dendrograptus* with an unusually high thecal spacing of 36 in 10 mm, and irregular and frequent branching from a robust stem region.

Fig. 6. A,B, Dendrograptus avonleaensis n.sp., respectively AM F114650 and holotype AM F114646a, both from BF14; *C, Dictyonema* cf. delicatulum, AM F114749, F14. Scale bars 1 mm.

Description. The overall colony shape may be irregularly dendroid, developed from a robust stem about 1 mm thick. Branching is frequent and irregular, at least once each 1–2 mm of stipe. The lateral stipe width decreases immediately away from the stem or main branches to approximately 0.30 mm; the dorsoventral width is about the same. Autothecae are visible where branches have been turned into the profile position, and seem to be of simple denticulate type, numbering 36 in 10 mm on both the specimens available. No trace of bithecae has been found. The specimen illustrated in Fig. 5B may have a relatively narrow holdfast at its base. The holotype has at least 21 terminal stipes after only 13 mm of growth, but the number at this stage could be much greater as several branches are broken.

Remarks. Most *Dendrograptus* species have thecae relatively widely spaced in the range of 12–20 in 10 mm, so *D. ashburniaensis* is unusual in this respect with its thecal spacing of 36 per 10 mm. *Dendrograptus* species are uncommon in the Silurian and we can equate our Bridge Creek specimens with none of them. *Dendrograptus parallelus* Shrock, 1928 from the Silurian of Indiana has a similar rhabdosome but the branching is much more widely spaced. *Dendrograptus phainotheca* Gurley, 1896 also has very widely spaced branching and an autothecal spacing of only 18 in 10 mm. Described Ordovician species have wider thecal spacings than *D. ashburniaensis* and mostly

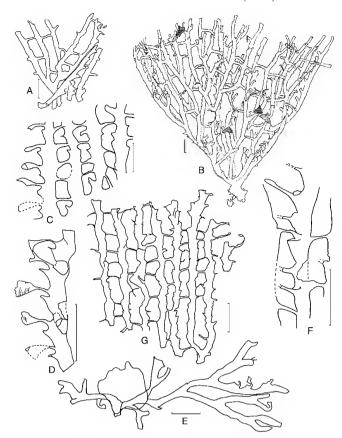


Fig. 7. A, Dictyonema venustum, AM F114751, BF28; B, Dictyonema williamsae n.sp., holotype AM F114565, W885; C–E, Dictyonema jenkinsi n.sp., respectively AM F114747, F14, holotype AM F114716, BF24; and AM F114761, F14, holdfast region attached to roughly circular object, possibly a pebble; F,G, Dictyonema paululum australis n.subsp., AM F114757, parts of holotype, BF14. Scale bars 1 mm; on B hatching indicates specimen obscured by sediment, stipple indicates badly preserved area, and horizontal shading indicates fractures in rock.

narrow stipes with more widely spaced branches. *Dendrograptus avonleaensis* n.sp. is the nearest form in general appearance but differs in having a much wider thecal spacing (see previous description).

The species described as *Dendrograptus* sp. B. by Rickards *et al.* (1995) has more widely spaced branching points than *D. ashburniaensis*, and *D.* sp. B. may be roughly compared with *D. parallelus*. Of the other Australian *Dendrograptus* species, *D.* sp. of Rickards & Wright (1997) from the *inexpectatus* or *kozlowskii* Biozone (Ludlow, Silurian) has a similar branching frequency but a much wider thecal spacing (15–20 in 10 mm). *Dendrograptus ashburniaensis* and *D. avonleaensis* are the best-preserved Australian *Dendrograptus* species so far described.

#### Dictyonema J. Hall, 1851

**Type species**. Gorgonia retiformis J. Hall, 1843; subsequently designated by Miller (1889).

**Remarks**. As there is often considerable difficulty, in the absence of holdfasts or siculate origins, in assigning a benthic or planktic mode to dendroid graptolite specimens, here we follow the traditional, conservative approach, as did Rickards *et al.* (1994), in using *Dictyonema* in its traditional sense to include planktic forms.

# Dictyonema cf. delicatulum Lapworth, 1881

Figs. 5G, 6C

cf. 1881. *Dictyonema delicatulum* Lapworth; Lapworth, p. 172, pl. 7, fig. 2a.b.

cf. 1928. *Dictyonema delicatulum*, Lapworth, emend.; Bulman, p. 51–52, pl. 6, figs. 7–11.

**Material**. AM F114648a, AM F114749 and AM F114769–71, all from F14, Bridge Creek.

Description. The best-preserved rectangular fragment of rhabdosome embraces eight stipes with several branching points, and measures 4×8 mm. Stipe spacing is about 20 in 10 mm, dissepiments (which are conspicuous) 14–18 in 10 mm, and the autothecal spacing 20–25 in 10 mm. Dissepiments vary from quite thread-like to a width of 0.10 mm, and are mostly disposed at right angle to the stipes. The lateral stipe width is 0.20–0.30 mm, but the dorsoventral stipe width cannot be measured in the absence of profile stipe views. There is, however, a suggestion of the autothecae, enabling a rough measurement, but the exact nature of the autothecal apertures cannot be ascertained, although one specimen (AM F114769) does show thecae with a long ventral denticle or spine.

Remarks. The material closely matches Bulman's (1928) redescription of the species, differing only in the dissepimental spacing (14–18 in 10 mm in the Australian specimens, compared with 10–12 in 10 mm in European specimens). We are, however, unsure of the exact nature of the autothecal apparatuses in our material, having established only that they are denticulate.

# Dictyonema williamsae n.sp.

Figs. 5D-F, 7B, 8A

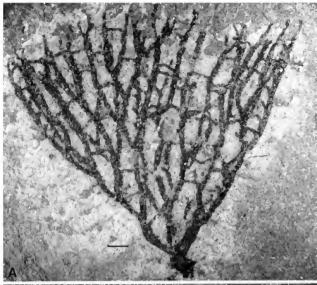
**Material**. HOLOTYPE AM F114565 and three PARATYPES AM F114652a-b, AM F114758 and AM F114772a-b, all from F14, Bridge Creek.

Derivation of name. After Norma Williams of "Ashburnia".

**Diagnosis**. Robust, conical *Dictyonema* rhabdosome, developed from a holdfast, each of four primary stipes with different branching patterns; stipes are connected by robust dissepiments, each of which is slightly arched distally; autothecae are aperturally isolated tubes without marked denticulation; autothecal spacing 13 in 10 mm; dissepimental spacing 6–7 in 10 mm; stipe spacing 8–12 in 10 mm; lateral stipe width maximum 0.30 mm; dorsoventral stipe width 0.60–0.70 mm.

**Description.** The rhabdosome is conical, some 14 mm high by 14 mm wide at the aperture of the cone. It derives from a small basal disc or holdfast. The most striking feature of the colony is the rectangular interstipe spaces defined by robust dissepiments and stipes of not much greater width; dissepiments are 0.15–0.20 mm wide and stipes in lateral view 0.15–0.30 mm. Of the several main stipes, which arise from the holdfast region, two produce at least 27 of the 34 peripheral stipes, so that one could say that at least three quarters of the cone is built by branchings from only two stipes. There are no obvious branching zones.

When seen in full profile the autothecae are aperturally isolated but without marked denticulation (Fig. 5D,E). In places they are difficult to distinguish from partially



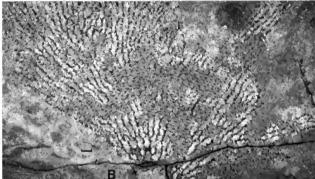


Fig. 8. A, Dictyonema williamsae n.sp., holotype AM F114565, F14; B, Dictyonema falciferum, AM F114750, F14. Scale bars 1 mm.

preserved dissepiments which have a similar width; it is possible, though unproven, that the dissepiments are actually autothecal transfers from one stipe to the adjacent stipe.

Remarks. Dictyonema williamsae is an unusual form having a low thecal spacing which eliminates comparison with most other dictyonemids. Dictyonema inequabile Bulman from the late Llandovery of Scotland has a similar arrangement of stipes and rhabdosome, but differs in having a less regular meshwork and very variable lateral stipe widths and equally variable dissepimental widths. The autothecal type and spacing is unknown in D. inequabile. However, D. inequabile is undoubtedly the closest form to D. williamsae, most dictyonemids having a much higher thecal spacing. Dictyonema obpyriforme (Gurley in Bassler, 1909) has a similar stipe arrangement but all measurements differ markedly. Many of the Silurian dictyonemids described by Bassler (1909) and Ruedemann (1947) have stipes that are much too robust for comparison with D. williamsae even when the stipes have rectangular interstipe spaces. Of the species described by Bouček (1957) Dictyonema elongatum is closest to D. williamsae in rhabdosomal and stipe dimensions, but its thecae appear to be simpler, its stipe spacing narrower (14–16 in 10 mm) and it dissepimental spacing wider (2-6 in 10 mm).

# Dictyonema falciferum Bulman, 1928

Figs. 5I, 8B, 9C, 10A

1928. *Dictyonema falciferum*, n.sp.; Bulman, p. 53–56, pl. 5, figs. 1–3, text-figs. 27–29.

Material. AM F114750 from F14, Bridge Creek.

**Description.** The flabellate appearance of this large, wellpreserved colony, some 27 mm by 40 mm, may be a preservational feature: there is a slight suggestion that it represents one half of a conical colony. The counterpart is, unfortunately, not available. There are at least 94 peripheral stipes developed, spaced at 16 in 10 mm, each with a lateral width of 0.20–0.25 mm. Branching zones are about every 1 mm proximally and 2–3 mm towards the periphery of the colony, complicated somewhat by local anastomosis. Dissepiments are spaced at 6-8 in 10 mm, possibly a little closer in places. Autothecae are denticulate but not otherwise ornamented. Bithecae are not developed with certainty, possibly rather bulbous aperturally, reflected in the slightly sinusoidal growth of the stipes when viewed dorsoventrally; the last feature is more conspicuous toward the periphery of the colony.

**Remarks**. This specimen differs only slightly from Bulman's type specimens, the stipes in the Bridge Creek specimens being a little more slender on average and the thecal spacing slightly wider (15? in 10 mm compared with 16–20 in 10 mm). In most aspects our form is very close indeed to the types, which were described from the upper Llandovery (approximately *crispus* Biozone) of Shropshire, Wales and Scotland (Bulman, 1928: 50). This is the first record of this species from Australia.

# Dictyonema venustum Lapworth, 1881

Figs. 7A, 9D, 10B-D

1881 Dictyonema venustum Lapworth; Lapworth, p. 171–172, pl. 7, fig. 1a–c.

1928 Dictyonema venustum, Lapworth, emend.; Bulman, p. 61–63, pl. 5, figs. 6–8, text-fig. 34.

**Material**. AM F114648a-b, AM F114649, AM F114717a-b and AM F114873, all from F14; AM F114751 from BF 28, all Bridge Creek.

**Diagnosis**. Large *Dictyonema* characterized by a striking rectangular meshwork of stipes and fairly robust dissepiments; at least 30 mm long, possibly conical, with irregular stipe branching; stipes 10–18 in 10 mm; denticulate autothecae spaced at 20–30 in 10 mm; dissepimental spacing 5–8 in 10 mm.

**Description**. Our largest specimen is a fragment of a large rhabdosome but it is not possible to say whether or not it is conical. A striking rectangular meshwork of stipes and fairly robust dissepiments typifies the colony. Stipes have a lateral width of 0.20–0.35 mm and a dorsoventral width of about 0.40 mm, whereas the dissepimental width is 0.10–0.25 mm. Stipe spacing ranges from 10–18 in 10 mm, the mean being 14–15 and the lower values nearer the proximal end. Stipe branching seems quite irregular. There is a limited amount of anastomosis in the stipe pattern. No bithecae have been detected.

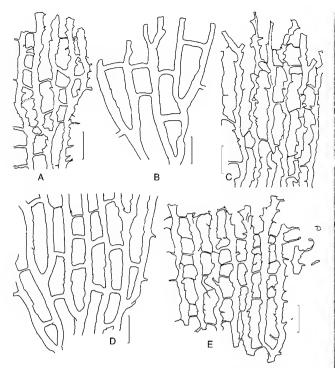


Fig. 9. *A–E*, illustrating contrasting stipe and dissepimental patterns in distal parts of colonies: *A, Dictyonema* cf. *delicatulum*, AM F114749; *B, Dictyonema williamsae* n.sp., AM F114565, holotype; *C, Dictyonema falciferum*, AM F114750; *D, Dictyonema venustum*, AM F114648a, F14; *E, Dictyonema paululum australis* n.subsp., holotype AM F114757. Scale bars 1 mm.

Remarks. In most respects our material is close to Bulman's (1928) redescription of the type and other material, differing only in having a slightly closer thecal spacing (20 in 10 mm compared with 16–17 in 10 mm) and slightly more slender dissepiments. The irregular branching mode is very similar to that on the Welsh and Scottish material described by Bulman (1928: p. 643), as is the stipe spacing, stipe widths and dissepimental spacing.

The largest specimen exhibits a damaged and repaired area (Fig. 10B, arrowed). In this region are two short, incomplete stipes whereas one very robust stipe tracks left to right, crosses one stipe and then anastomoses with the next one, which then terminates. The stipe crossed over by the robust, laterally-directed stipe continues to grow and fills the gap caused by the damage, so that by the rhabdosomal periphery a normal stipe arrangement is restored. The most likely explanation of the damage is that a hole was punched into the stipe array, separating the stipes and breaking off some of them.

### Dictyonema paululum australis n.subsp.

Figs. 7F,G, 9E, 12A

Material. HOLOTYPE AM F114757a-b and PARATYPES AM F114758 and AM F114773–4, all from BF14, Bridge Creek.

**Derivation of name**. Suggesting that it is a geographical subspecies.

**Diagnosis**. Conical *Dictyonema paululum* with 16 stipes in 10 mm; autothecae denticulate and spaced at 20 in 10



Fig. 10. A, Dictyonema falciferum, AM F114750, F14; B–D, Dictyonema venustum, respectively AM F114648 and AM F114873, both BF14, and AM F114751, BF28. Scale bars 1 mm; arrow on B indicates damaged area discussed in text.

mm; dissepiments spaced at 12–20 in 10 mm; stipe lateral width 0.20 mm and dorsoventral width 0.50 mm.

**Description**. The largest specimen is about 30 mm long and all the rhabdosomal fragments are characterized by slender stipes with a marked parallel arrangement connected by very slender dissepiments of 0.05 mm. Branching is very approximately zoned, every 1.5–2.5 mm, being more widely spaced distally. Dissepimental spacing is closest distally, at 20 in 10 mm, about one per autotheca, but proximally may rise to 12–13 in 10 mm. The autothecae are certainly denticulate, even spinose in profile, and the termination may possibly be spatulate rather than pointed. It is difficult to distinguish autothecal processes from dissepiments in this material. The overall appearance of the stipes is gently undulating with a serrated margin in places (Fig. 7G).

**Remarks**. Dictyonema paululum australis occurs at the same late Llandovery level as the nominate subspecies and, although very elegant and slender, is fractionally more robust than that form, with a more varied dissepimental spacing. In the nominate subspecies, the stipe spacing is slightly wider (16 in 10 mm compared with 20 in 10 mm) and the rectangular interspaces are narrower and often longer. The differences seem consistent in all material, and we regard D. p. australis as a geographical subspecies of D. paululum Bulman, 1928.

## Dictyonema jenkinsi n.sp.

Figs. 7C-E, 11A,B

**Material**. HOLOTYPE AM F114716 and PARATYPES AM F11461, AM F114747–8 and AM F114776–8, all from F14, Bridge Creek.

**Derivation of name**. In honour of Dr Chris Jenkins who collected many of the graptolites in our collections.

**Diagnosis**. Large, ?conical *Dictyonema* rhabdosome developed from basal holdfast; thecae with unique, platelike outgrowths of dorsal, apertural processes; autothecal apertures slightly isolated; bithecae bulbous aperturally.

**Description**. One rhabdosomal fragment (Fig. 7E) is of a holdfast with three or four main stipes developed from it; stipe division is close to the holdfast and, although this specimen is preserved in "plan" view, it suggests that a conical rhabdosome develops from the holdfast. Another large fragment of rhabdosome, of which Fig. 7C is a part, indicates an overall large colony perhaps 25 mm long. Stipes are spaced at 14 in 10 mm, have a lateral width of about 0.50 mm, and are connected by hair-like dissepiments spaced at 18–20 in 10 mm and by occasional anastomosis. The stipe spacing is, therefore, slightly closer than the autothecal spacing, which is 16 in 10 mm. The autothecae have slightly isolated thecal apertures, a denticulate ventral apertural process (Fig. 7D) and a conspicuous dorsal apertural process, composed of fuselli, which grows to a plate-like form expanding away from the apertural region.

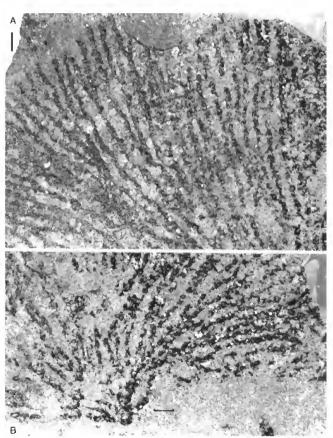


Fig. 11. A,B, Dictyonema jenkinsi n.sp., AM F114748, respectively distal thecae and proximal end close to holdfast, F14. Scale bars 1 mm.



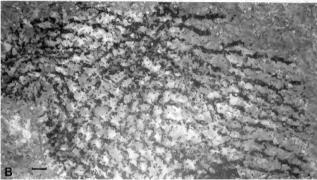


Fig. 12. A, Dictyonema paululum australis n.subsp., AM F114757, holotype, BF14; *B, Dictyonema warrisi* n.sp., holotype AM F114647a, F14. Scale bars 1 mm.

Sometimes it hangs downward slightly, presumably overhanging the apertural region. The dorsoventral width is 0.80 mm, excluding the large process, but up to 1.30 mm including it. Bithecae can be detected on the holotype as bulbous growths positioned dorsally of the autothecal apertural region; they alternate along the stipe (Fig. 7D).

**Remarks**. The autothecal processes make *D. jenkinsi* a unique species. Similar plate-like growths are developed on *D. peltatum* Wiman, 1901, but these are modified ventral apertural processes. The hydrodynamic function may be similar, of course, as suggested by preliminary work by one of us (R.B.R.). The bithecae may be of Bulman's (1928) type 5; that is, not dissimilar to the bithecae in *D. cavernosum* Wiman, 1901 (see Bulman & Rickards, 1966).

### Dictyonema muirae n.sp.

Fig. 13A-D

**Material.** HOLOTYPE AM F114762 and PARATYPES AM F114763–4 and AM F114775, all from F14, Bridge Creek. PARATYPE AM F14779 from BF24, Wallace Creek.

**Derivation of name**. After Lucy Muir, in recognition of her skilled graptolite collecting.

**Diagnosis**. *Dictyonema* with unusually close thecal spacing of 40 in 10 mm, of denticulate autothecae, and with very unusual isolated, curved bithecae; sparse dissepiments.

Description. The rhabdosome grows from a holdfast with rapid and irregular branching taking plate (Fig. 13D). Irregular branching is maintained in the specimens we have, and perhaps because of the frequency of branching, dissepiments are difficult to identify and possibly few in number. Stipe spacing is 14–20 in 10 mm depending upon how divergent the growth is at any point. The dorsoventral stipe width is about 0.60 mm, and the lateral stipe width 0.30–0.40 mm. The autothecae are markedly denticulate (Fig. 13B) and are spaced at 40 in 10 mm. Associated with the autothecae (Fig. 13C) are curved, narrower tubes, the apertures of which face distally. These are probably bithecae and they may be a modified form of Bulman's (1928) Type 5 where the bithecal apertural region extends in an isolated manner. The overall colony form is not known.

**Remarks**. The combination of very close autothecal spacing with unusual bithecae makes *D. muirae* a unique, unusual species of *Dictyonema*. The irregular, frequent, and divergent branching, coupled with the presence of dissepiments, supports attribution to *Dictyonema* rather than *Callograptus*. The individual stipes look not unlike robust *Dendrograptus* species.

### Dictyonema warrisi n.sp.

Figs. 12B, 13E-G

Material. HOLOTYPE AM F114647a-b and PARATYPES AM F114629b and AM F114717, all from F14, Bridge Creek.

**Derivation of name**. After Dr Bevan Warris who first mapped the Angullong Syncline in detail.

**Diagnosis.** Unusual *Dictyonema*, ?conical, 3 cm long, with pronouncedly spinose autothecae, closely spaced at 28 in 10 mm; lateral stipe width 0.20–0.30 mm; dorsoventral stipe width 0.20–0.35 excluding spines which may be 1 mm long.

**Description**. The largest rhabdosome, possibly conical, is 30 mm long and 14 mm wide. A second, smaller (15 mm by 7 mm) specimen, possibly part of the same conical rhabdosome, crosses the first. The overlap area of the two creates an initially misleading *Desmograptus* appearance. On this large specimen the spinose thecae are difficult to see but are present. Dissepiments vary from fine and hairlike to more robust and irregular (Fig. 13E). Dissepimental spacing is about 12 in 10 mm but rather variable from place to place. The isolated stipe fragment (Fig. 13F) is in full profile and shows the ventral apertural spines well though not to full length. The bithecal apertures open in the angle between the autothecal aperture and the ventral wall of the next autotheca (thecae 1, 3, and 5 on Fig. 13F). They are of Bulman's (1928) type 4.

**Remarks**. Very few *Dictyonema* species are known with long autothecal spines. Rickards *et al.* (1995, p. 22, fig. 14G) illustrated *Dictyonema* sp. E with long, bifurcating ventral spines (see description of *Dictyonema* sp. 1 below). *Dictyonema warrisi* is distinct from that form in that the spines do not bifurcate.

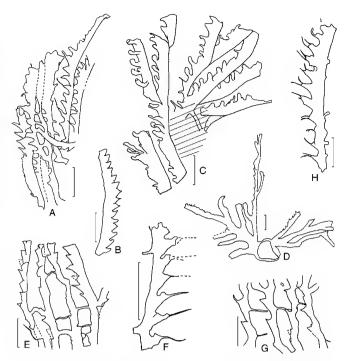


Fig. 13. A–D, Dictyonema muirae n.sp., respectively AM F114763, BF14, AM F114775, F14, holotype AM F114762, F14, and AM F114764, BF14 proximal part of colony attached to pebble of phosphate; *E–G*, Dictyonema warrisi n.sp., respectively AM F114647, F14, holotype AM F114717, W885 and AM F114647, F14, with stipes more proximal than E; *H*, Dictyonema sp. 1, AM F11475, F14. Scale bars 1 mm; shading on *C* indicates badly preserved area.

### Dictyonema sp. 1

Fig. 13H

Material. AM F114754 from F14, Bridge Creek.

**Description**. One small stipe fragment shows 10–11 thecae spaced at 20 in 10 mm, each provided with two spines. It is not certain, but it seems likely, that these spines grow from the ventral region of the autothecal aperture. No traces of bithecae are visible. The dorsal wall shows the bases of 3–4 dissepiments giving a dissepimental spacing of about 8 in 10 mm. The dorsoventral width excluding processes is up to 0.75 mm, and up to 1.25 mm including spines. It is uncertain whether the spines are formed from bifurcation of one ventral denticle, or whether two spines arise independently from the ventral apertural wall.

**Remarks.** *Dictyonema* sp. 1 differs from *D. warrisi* in having a wider thecal spacing (20 compared with 28 in 10 mm) and in having two thecal spines. *Dictyonema* sp. E of Rickards *et al.* (1995: 22, fig. 14G) has a bifurcating ventral process and a thecal spacing of 30 in 10 mm. This latter form is from the *nilssoni* Biozone (Ludlow) and the thecal spines are more like those of *D. cervicorne* Holm, 1890, from the Ordovician of Scandinavia (although lacking the bulbous bithecae of that form) than those of *D. warrisi*.

# Callograptus J. Hall, 1865

Type species. Callograptus elegans J. Hall, 1865.

# Callograptus bridgecreekensis n.sp.

Figs. 14A, 15A,B

Material. HOLOTYPE AM F114569a-b from F14, Bridge Creek.

**Derivation of name**. After the stream at the type locality.

**Diagnosis.** Callograptus with a robust stem, consisting of numerous tubes, 10 mm long and 1.2 mm wide; no dissepiments; spacing of sharply denticulate autothecae 30–35 in 10 mm, bithecae small, inconspicuous tubes.

**Description**. A single, large rhabdosome 35 mm long by 27 mm wide is developed from a robust stem region, itself about 10 mm long and 1.2 mm at its widest. The stem may originate from a small holdfast about 2 mm wide. The stem comprises a considerable bundle of tubes, some ending as thecal apertures along its length (Fig. 15B). The rhabdosome has over 50 terminal stipes preserved. The stipes are parallel and divergence at branching points is at a low angle: stipe frequency is 19-21 in 10 mm. Branching is frequent and irregular but a relatively small number of "main stipes" seem to give rise to the many terminal stipes. There are four, possibly five "main stipes" on the specimen: one (possibly two) arises quickly at the top of the stem region; the other three develop within 5 mm of the top of the stem. This arrangement of fan-like fronds, coupled with the presence of a robust stem, suggests an overall fan-shaped rather than conical colony. There are no dissepiments. Lateral stipe width proximally is 0.40-0.60 mm and most distally 0.20-0.30 mm. The dorsoventral stipe width is 0.40-0.50 mm. Autothecal spacing is 30-35 in 10 mm. The autothecae are sharply denticulate, possibly slightly spatulate, but not spinose. Bithecae are small, inconspicuous tubes opening in the axil between autothecal aperture and the free ventral wall of the next autotheca.

Remarks. The arrangement of fan-like branches is not uncommon in Callograptus (e.g., the type species C. elegans), and recalls to some extent Licnograptus Ruedemann, 1947 (wherein thecal details are unknown). Callograptus, like *Dendrograptus*, is uncommon in the Silurian. Callograptus bridgecreekensis differs from the two Silurian forms briefly discussed by Bulman (1928), and from the three species described by Bouček (1957): C. conjunctus Bouček exhibits stipe anastomosis and the stipes are more robust and widely spaced; C. flabellatus Bouček (? = Dictyonema) has numerous dissepiments; and C. scopatus Počta is a markedly more robust species with very widely spaced stipes. Of the North American forms described by Bassler (1909), C. minutus Spencer, 1878, C. multicaulis Spencer, 1878 and C. niagarensis Spencer, 1878 (see description below) have small, bushy rhabdosomes, and C. strictus Gurley, 1896 (? = Dictyonema) has numerous dissepiments. Ruedemann (1947) considered an additional species, C. pulchellus Shrock, 1928 (see also Rickards & Wright, 1997), which has dissepiments but similar dimensions. The form described as Callograptus ?pulchellus Shrock subsp. 1 by Rickards & Wright (1997,

fig. 4D) has more undulating, divergent stipes than *C. bridgecreekensis*, whereas *C. ?pulchellus* Shrock subsp. 2 of Rickards & Wright (1997) is insufficiently known but is possibly referable to *C. bridgecreekensis* (although subsp. 2 is from the late Ludlow).

# Callograptus rigbyae n.sp.

Fig. 14B,C

**Material**. HOLOTYPE AM F114651a-b, from BF28 from an unnamed tributary W of Bridge Creek; and PARATYPE AM F114643 from W885, Bridge Creek.

**Derivation of name**. After Dr S. Rigby, well-known graptolite worker.

**Diagnosis.** Small, robust *Callograptus* with small holdfast or short stem; usually preserved in "plan" view, branching in well-marked zones, six of which give a 10 mm colony spread; dissepiments absent; autothecae 20 in 10 mm approximately.

Description. The rhabdosomes are spread in a "plan" view but are sufficiently well-preserved to conclude that dissepiments are absent. Stipes have a lateral width of 0.20–0.30 mm and there are five branching zones in a distance of 5 mm from the origin resulting in rhabdosomes about 10 mm in diameter with 40 or so preserved peripheral stipes. Autothecae appear to be simple non-denticulate tubes spaced at approximately 20 in 10 mm: near the autothecal apertures the periderm is thin. At branching points the axil is sometimes infilled with the thin-walled autotheca terminating the preceding stipe. No bithecae have been seen. The origin is unclear but may consist of a small holdfast or a very short, twisted stem.

**Remarks**. Callograptus rigbyae resembles none of the Callograptus species discussed under the previous description. The obvious lack of a conspicuous stem region distinguishes it from C. bridgecreekensis n.sp. There is a presumed superficial resemblance with the Early Ordovician Staurograptus, which is a siculate, planktic genus. There is also some similarity between C. rigbyae and Dictyonema sp. A of Rickards & Wright (1997) from the late Ludlow near Mumbil, NSW, but the latter has well-developed dissepiments.

# Callograptus ulahensis n.sp.

Figs. 16A, 17A

**Material**. HOLOTYPE AM F114760 and PARATYPE AM F114780, both from BF15, S of junction of Four Mile Creek and Bridge Creek.

**Derivation of name**. After Ulah property.

**Diagnosis**. *Callograptus* with fan-like stipe clusters, connected by uncommon, hair-like dissepiments; branching in rough zones resulting in slender parallel stipes; and very simple autothecae spaced at 20 in 10 mm.

**Description.** Both specimens exhibit rather slender stipes 0.20–0.30 mm in lateral width and 0.40–0.50 mm in dorsoventral width. The autothecal apertures are simple, non-denticulate, spaced at 20 in 10 mm and the apertures

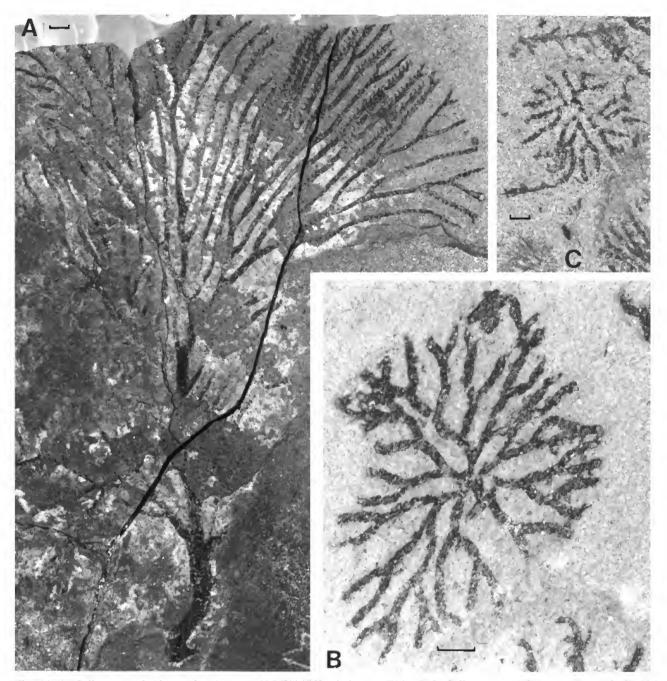


Fig. 14. A, Callograptus bridgecreekensis n.sp., AM F114569a, holotype, F14; B,C, Callograptus rigbyi n.sp., respectively AM F114651a, holotype, BF28, and paratype AM F114643, W885. Scale bars 1 mm. Note that in Fig. 14B the isolated autothecae of Cyclograptus? australis can be seen at bottom right and on Fig. 14C a specimen of Acanthograptus praedeckeri occurs at the top.

themselves occupy almost half of the dorsoventral width. The larger specimen (Fig. 16A) suggests broad branching zones. The stipes are connected by irregular and uncommon hair-like dissepiments which may be more common in the regions of the branching zones. No bithecae have been detected.

**Remarks**. This very simple and slender-stiped *Callograptus* bears no resemblance to any of the Silurian callograptids reviewed under the Remarks section above of the description of *C. bridgecreekensis*. *Callograptus ulahensis* has a different branching pattern to *C. bridgecreekensis* and a much wider thecal spacing (20 in 10 mm compared with 30–35 in 10 mm).

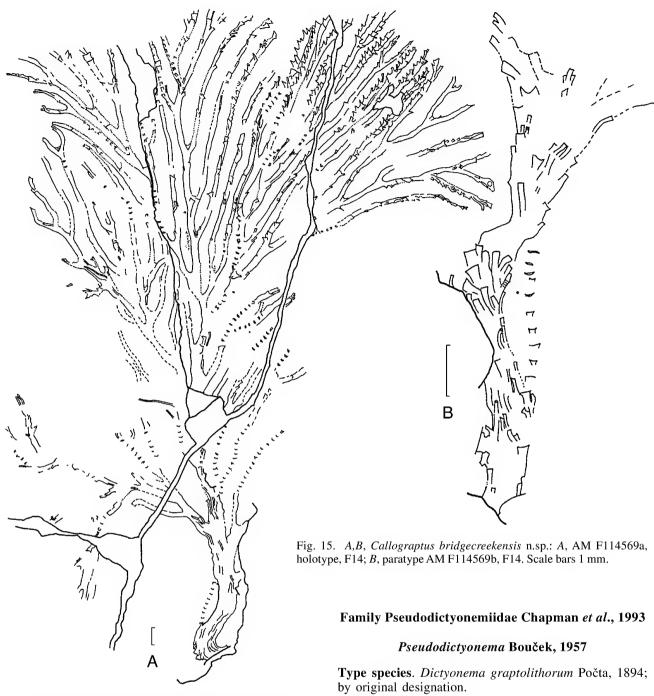
### Callograptus cf. niagarensis Spencer, 1878

Fig. 16B

cf. 1878 *Callograptus niagarensis* Spencer, pp. 458, 463. cf. 1909 *Callograptus niagarensis* Spencer; Bassler, p. 13–14, fig. 15. (A full synonymy was given by Bassler [1909]).

Material. AM F114739 from F14, Bridge Creek.

**Description.** A single rhabdosome with the proximal region missing shows a series of diverging, wavy stipes, probably compound to judge from the striations along their length, unconnected by dissepiments and branching in an irregular manner. The stipes are rather broad proximally, about 0.50



mm, and more distally narrow to 0.25 mm, and appear to be constructed of long narrow tubes although the distal terminations of these tubes—the apertures—are not seen. Autothecae may be simple, denticulate spaced at ?20 in 10 mm.

Remarks. Callograptus niagarensis is known from only one specimen from the Niagaran dolomites and shales. The holotype appears to have a central dominant stipe: unfortunately this cannot be ascertained in our specimen. The wavy and diverging nature of the stipes is very similar in both specimens, but the Bridge Creek specimen has stipes which are a little more robust. Like the holotype, the Bridge Creek specimen shows bundles of tubes comprising the stipe, though not clearly. The original description suggests about 16 (auto)thecae in 10 mm (40 to the inch) which is not too different from our specimen which might be of the order of 20 in 10 mm.

### Pseudodictyonema graptolithorum (Počta, 1894)

Fig. 16C-E

1894 Dictyonema graptolithorum n.sp.; Počta, p. 196, pl. 9, fig. 14.

1957 Dictyonema (Pseudodictyonema) graptolithorum Počta, 1894; Bouček, p. 69–70, pl. 7, pl. 8, figs. 4–6, text-fig. 27a–c.

Material. AM F114753, AM F114755 and AM F114645, all from F14, Bridge Creek.

**Diagnosis**. *Pseudodictyonema* with characteristically ropy, compound stipes, a rectangular meshwork defined by stipes and robust dissepiments; stipes spaced at 14–16 in 10 mm; dissepiments 8–13 in 10 mm; stipes 0.30–0.50 mm wide; autothecal spacing about 14–15 in 10 mm.

**Description**. The stipes are markedly parallel and the meshwork strikingly rectangular. The largest rhabdosome in our collection is 15 mm long by 25 mm wide, probably developed from a short stem. The autothecae have isolated apertural regions at the ends of long tubes which, with numerous others, make up the ropy texture of the stipes. Despite the obvious complexity of the stipes the autothecal apertures are spaced regularly at 14–15 in 10 mm. Dissepiments vary from very fine to quite robust and it is likely that some involve transfer of the thecal tubes from one stipe to the next. The spacing is also variable but in the range 8–13 in 10 mm. One specimen, AM F114645, has dissepiments spaced as high as 12–13 in 10 mm in places.

**Remarks**. The only difference between our material and the Czech types is that the types have a higher dissepimental spacing (15–16 in 10 mm given by Bouček, 1957); his figures 27a and 27c have much lower dissepimental spacing than given in his text (actually 5–6 in 10 mm).

# Family Stelechocladiidae Chapman et al., 1993

### Stelechocladia Počta, 1894

**Type species**. *Stelechocladia subfruticosa* Počta, 1894, subsequently designated by Bouček (1957).

### Stelechocladia praeattenuata n.sp.

Figs. 17B, 19A,B

**Material**. HOLOTYPE AM F114743a-b, from BF28, W tributary of Bridge Creek. PARATYPES AM F114765 from BF14, Bridge Creek; AM F114781 from F14, Bridge Creek; AM F114782a-b from BF18; AM F114783 from F19, Four Mile Creek; and AM F114784 from BF18.

**Derivation of name**. To reflect its earlier occurrence than the most similar species, *Stelechocladia attenuata* Bouček, 1957.

**Diagnosis**. Robust *Stelechocladia* with dominant main stipes and shorter, intermediate, finer stipes quite regularly arranged; 10–14 stipes in 10 mm; autothecal spacing 30–40 in 10 mm; rhabdosome developed from broad holdfast; stipes with proximal lateral width of 1.0 mm at most; dorsoventral width 0.70–0.90 mm.

**Description**. The rhabdosome develops from a holdfast 3– 5 mm across; although detailed growth close to the holdfast is not clear, three or four main stipes seemingly arising from an amorphous mass of tissue. The mains stipes are initially up to 1 mm wide (lateral width) though usually less than this. More distally they gradually become narrower reaching 0.25-0.30 mm. Intermediate stipes are similarly tapered. However, when seen in profile view, when the denticulate autothecae are clearly visible, the dorsoventral width is fairly constant at 0.70–0.90 mm. Branching from the main stipes is frequent but irregular, and it tends to be from one side of the main stipe. Branching from the main stipes takes place every 0.50-1.50 mm. The result of the branching is a striking array of spike-like stipes, quite unconnected (except at the branching points) with shorter, intermediate stipes filling the spaces between main stipes. Many intermediate stipes are rather short and seem to be positioned merely to fill a space between two adjacent but distally converging longer stipes. No bithecae have been detected.

**Remarks.** Stelechocladia attenuata from the Přídolí of the Czech Republic is undoubtedly the closest species but is much larger and altogether more robust than in *S. praeattenuata*, and also has a wider autothecal spacing (25 in 10 mm compared with 30–40 in 10 mm: see Kraft, 1984).

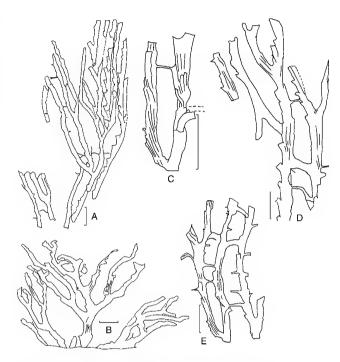


Fig. 16. A, Callograptus ulahensis n.sp., AM F114760, holotype, BF15; B, Callograptus niagarensis, AM F114739, W885; C–E, Pseudodictyonema graptolithorum, respectively AM F114755, AM F114753 and AM F114645, all from F14. Scale bars 1 mm.

### Family Acanthograptidae Bulman, 1938

### Acanthograptus Spencer, 1878

**Type species**. Acanthograptus granti Spencer, 1878; by original designation.

### Acanthograptus praedeckeri n.sp.

Figs. 17C,D, 18A, 19C, 20A-E

Material. HOLOTYPE AM F114792a-b, from BF28, Bridge Creek. PARATYPES AM F114629a, AM F114718, AM F114740a-b, AM F114741, AM F114785–89 and AM F114791, all from F14; AM F114742 from BF29, W tributary of Bridge Creek; AM F114630 from F6, Wallace Creek; AM F114568a-b, AM F114741, AM F114790–1 and AM F114793–4, all from BF28, W tributary of Bridge Creek.

**Derivation of name**. To reflect its earlier occurrence than the low Ludlow species *A. deckeri*, which it resembles.

**Diagnosis.** Large, flabelliform *Acanthograptus* in which the main stipes grow from a robust stem region; twigs and

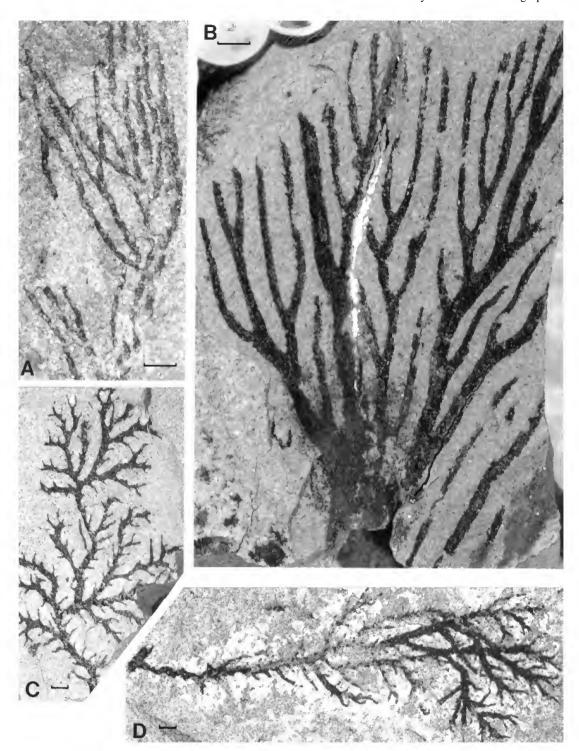


Fig. 17. A, Callograptus ulahensis n.sp., AM F114760, holotype, BF15; B, Stelechocladia praeattenuata n.sp., AM F114743, holotype, BF28; C,D, Acanthograptus praedeckeri praedeckeri n.sp., respectively AM F114792, holotype, BF28 and AM F114568a, F14. Scale bars 1 mm.

secondary branches spread to all available space; 8–14 twigs in 10 mm; twigs 0.70–1.0 mm long; main stipe 0.40–0.50 mm wide; branching every 0.50–1.50 mm.

**Description**. In the best preserved specimens there is no physical overlap of adjacent stipes. Rather, the overall branching pattern grows and spreads in all directions to fill the available space. Thus the rhabdosome, although bushlike in appearance, is actually flabelliform. In sections of

stipe where no branching takes place the twigs alternate from side to side in classic *Acanthograptus* fashion. Each twig usually comprises more than one autothecal tube although some seem to terminate in a single tube. However, the twig arrangement breaks down frequently because numerous dichotomies of the stipes occur, spaced at 0.50–1.50 mm intervals. All the stipes appear to be compound with numerous elongate tubes visible.

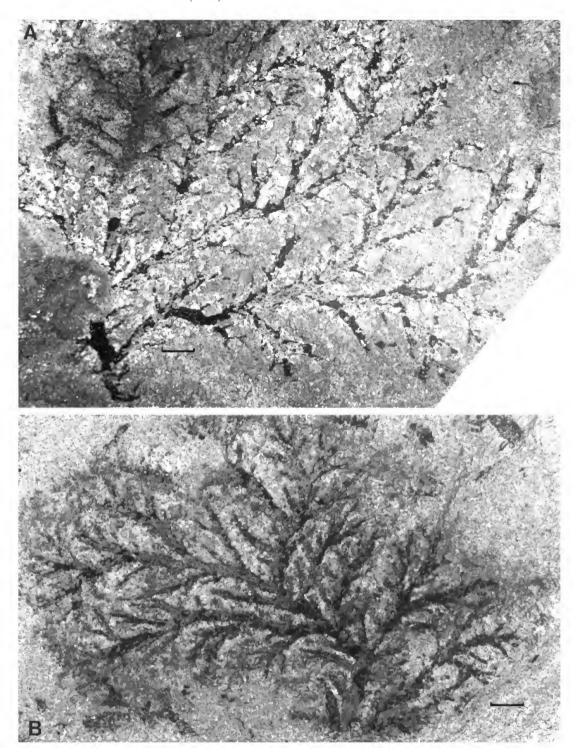


Fig. 18. A, Dictyonema warrisi n.sp., AM F114629b, F14; B, Thallograptus christoffersonae n.sp., AM F114644, W885. Scale bars 1 mm.

Remarks. Acanthograptus praedeckeri n.sp. has too few twigs and too great a stipe width for comparison with A. aculeatus Počta, as well as having a bushier rhabdosome altogether. Acanthograptus deckeri from the low Ludlow has a similar rhabdosomal appearance, but the twig arrangement is less regular and all the stipes more compound and more robust. Acanthograptus praedeckeri is very similar to Thallograptus christoffersonae described below, and the differences are listed under the Remarks section of the latter.

# Acanthograptus praedeckeri minimus n.subsp.

Fig. 20F

Holotype. AM F114630, from F6, Wallace Creek.

**Derivation of name**. To indicate smaller dimensions than the nominate subspecies.

**Diagnosis**. Acanthograptus praedeckeri differing from the nominate subspecies in: its much smaller form with narrower stipes, the more open "space coverage" by the branching, and with twig spacing twice as frequent.

**Description**. The single well-preserved rhabdosome shows several well-developed branches and numbers of twigs. The stipes are uniformly narrow at 0.20 mm yet clearly compound with bundles of long narrow tubes. It is possible that some of the twigs may terminate with a single autotheca but parts of some twigs have more than one thecal tube involved. Some thecae appear to open on the main stipes, their apertures adpressed to the surface. Twigs are 0.30–0.60 mm long, usually directed at about 45° to the stipe axis; twig spacing more than 20 in 10 mm.

**Remarks**. Although having the same general appearance as the type subspecies, *A. p. minimus* is a much smaller form with narrower stipes and the "space coverage" by the branching is more open. It is difficult to give a twig spacing accurately, because of the numbers of branches, but twig spacing is certainly twice as frequent as in the type subspecies.

# Thallograptus Ruedemann, 1925

**Type species**. *Dendrograptus? succulentus* Ruedemann, 1905, by original designation.

# Thallograptus christoffersonae n.sp.

Figs. 18B, 22A,B

**Material**. HOLOTYPE AM F114746, W885 (approximately = BF14 and F14), Bridge Creek. PARATYPES AM F114644, W885 and AM F114765, BF14; and numerous other specimens from F14, BF24, BF28, and BF29, all uppermost Llandovery.

**Derivation of name**. After Ruth Christofferson of "Avon Lea".

**Diagnosis**. *Thallograptus* with very bushy dendroid appearance, fan-shaped; stipes no more than 0.60 mm wide, branching every 1 mm or less; about 10 stipes per cm; twigs at rate of 12 per cm, up to 1 mm long, terminating as one autothecal tube; autothecae 0.10–0.15 mm wide; bithecae 0.03–0.04 mm wide.

**Description**. The rhabdosome, measuring up to 25 mm wide and 15 mm long on the largest specimens, is probably fanshaped because despite the dendroid, fan-shaped appearance stipes do not overlap but fill the available space. A holdfast has not been identified. At their thickest the stipes are about 0.60 mm wide, and branching takes place regularly, usually with intervals of less than 1 mm between branches. Branches diverge in such a manner that the available space is filled. There is no anastomosis. Twigs occur between branching points and are spaced at around 10-12 per cm with an individual length of up to 1 mm. They terminate in single autothecal tubes having a diameter of 0.10-0.15 mm and unornamented apertures. Along the main stipes bundles of up to 6 autothecae are visible in the ropy stipe texture, implying that there are considerably more in any one cross section of stipe. Bithecae are seen occasionally as diminutive tubes, 0.03-0.04 mm wide, irregularly positioned.

**Remarks.** The closest species seems to be *T. elegans* Bouček, 1957, which has a similar growth pattern of the stipes. In this form, however, the stipes are much thicker, and they thin and thicken at branching points which does not occur

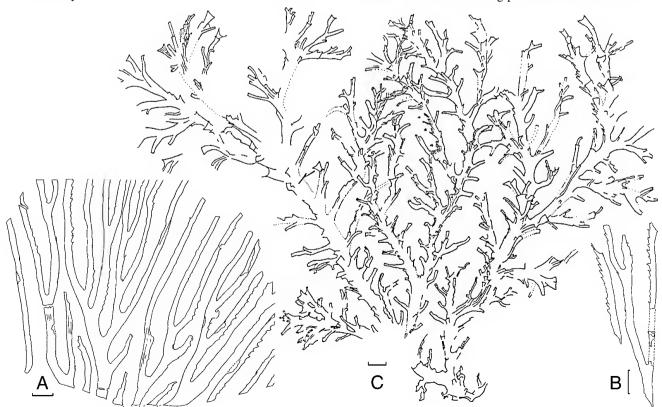


Fig. 19. A, B, Stelechocladia praeattenuata n.sp.: A, AM F114743, holotype, and B, AM F114744, both BF18; C, Acanthograptus praedeckeri praedeckeri n.sp., AM F114629a, F14. Scale bars 1 mm.

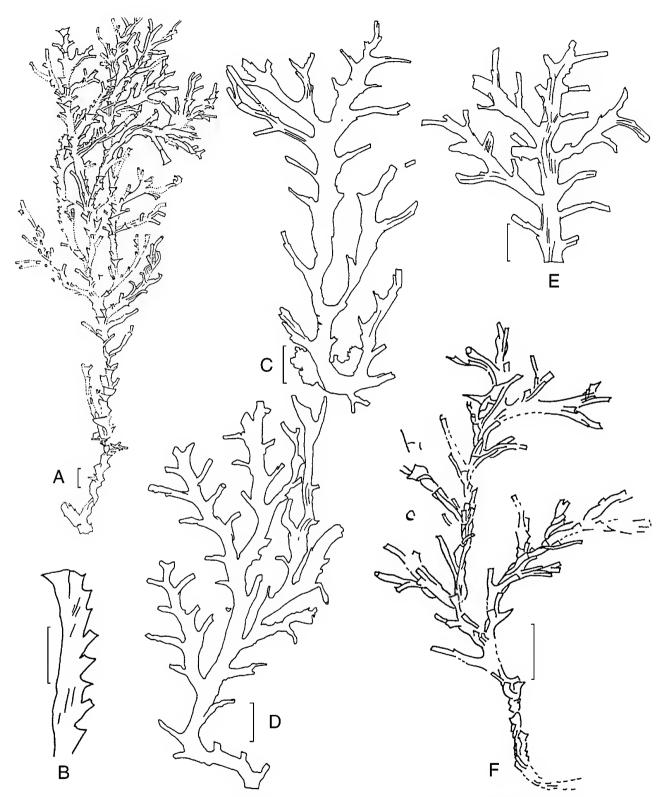
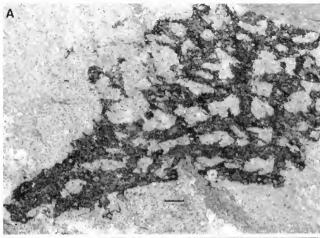


Fig. 20. A–E, Acanthograptus praedeckeri praedeckeri n.subsp., respectively AM F114568, AM F114568, AM F114741, AM F114742 and AM F114740, all from F14; F, Acanthograptus praedeckeri minimus n.subsp., AM F114630, F6. Scale bars 1 mm.

in *T. christoffersonae*. Other measurements, such as stipe spacing and branching frequency, also differ. *Acanthograptus praedeckeri* n.sp. is also similar in rhabdosomal form (and it is interesting that Bouček (1957: 102) referred his new species *A. deckeri* inadvertently to *Thallograptus!*). *Acanthograptus praedeckeri* n.sp. differs from *Thallograptus christoffersonae* n.sp. in having a definite twig

system where each twig is composed of several thecae, the twigs are shorter, and branching is much less frequent. *Thallograptus densus* Kraft, 1979 is another similar species but differs in having more parallel and more densely arranged stipes; it occurs in the *sedgwickii* Biozone (Llandovery). *Thallograptus elegans* is a Wenlock to Ludlow species.



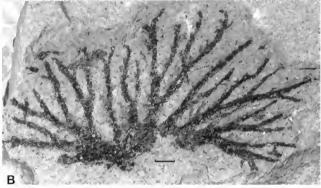


Fig. 21. *A, Koremagraptus obscurus* n.sp., AM F114745, holotype, BF28; *B, Cyclograptus? australis* n.sp., AM F114651, holotype, BF28. Scale bars 1 mm.

### Koremagraptus Bulman, 1927

Type species. Koremagraptus onniensis Bulman, 1927, by original designation

## Koremagraptus obscurus n.sp.

Figs. 21A, 22C

**Material**. HOLOTYPE AM F114745, the only specimen, from BF28, W tributary of Bridge Creek.

**Diagnosis**. *Koremagraptus* with growth direction of individual stipes difficult to ascertain due to complex and rapid anastomosis; most thecal apertures, with a diameter of 0.15 mm, are located on stipe walls and only rarely isolated.

**Derivation of name**. Reflecting the complex anastomosis of stipes.

**Description**. The large fragment of rhabdosome exhibits a complex mass of anastomosing stipes. Each stipe is clearly composed of numerous thecal tubes. Most thecal apertures are located on the stipe walls and only rarely are isolated. In Fig. 22C the arrows indicate the growth directions of three stipes. It is immediately obvious that in a distance of only 3 mm several instances of complex anastomosis occur. Most anastomosis seems to involve the transfer from one stipe to another of whole bundles of tubes. The tube apertures—presumed autothecal apertures—have a diameter of 0.15 mm. There is a suggestion that the stipes and thecal tubes are thin walled.

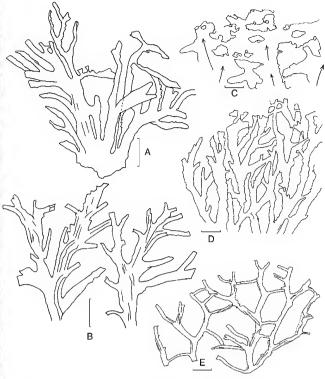


Fig. 22. *A,B. Thallograptus christoffersonae* n.sp.: *A*, AM F114765, stipe development from basal holdfast, BF14 and *B*, AM F114746, holotype, F14; *C, Koremagraptus obscurus* n.sp. AM F114745, holotype, BF28; *D, Koremagraptus elegantulus* n.sp. AM F114752, holotype, W885; *E, Reticulograptus thomasi* n.sp. AM F114756, holotype, BF28. Scale bars 1 mm.

Remarks. Koremagraptus obscurus n.sp. has the characteristics of previously-described koremagraptids but taken to extremes in that the growth direction of individual stipes is difficult to ascertain at any one point, so great is the anastomosis. Koremagraptus obscurus can be contrasted, for example, with K. elegantulus n.sp., which is a more typical koremagraptid in its stipe arrangement. It is possible that other fragments in our collections might be referable to K. obscurus because small pieces of complex, thin-walled stipe fragments are not uncommon. Koremagraptus flexuosus Bouček, 1957 from the basal Devonian has a similar stipe pattern but is less densely connected.

### Koremagraptus elegantulus n.sp.

Fig. 22D

Material. HOLOTYPE AM F114752 from F14, Bridge Creek and PARATYPE AM F114717a-b from W885, Bridge Creek.

**Derivation of name**. Reflecting the nature of the stipe pattern.

**Diagnosis**. *Koremagraptus* with gently diverging and anastomosing robust compound stipes 0.50–0.70 mm across; lacks recognizable autothecae.

**Description**. The large portion of rhabdosome measures 35 mm by 25 mm, and is typified by gently diverging and anastomosing robust stipes, each about 0.50–0.70 mm across except at points of anastomosis where they are wider. A number of twig-like terminations occur, often extending into the spaces formed by the anastomosing main stipes. Some of the "twigs" may terminate as single autothecal

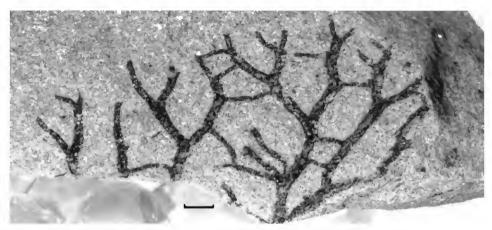


Fig. 23. Reticulograptus thomasi n.sp., AM F114756, holotype, BF28. Scale bar 1 mm.

tubes. Autothecae have not been readily identified, however, and no thecal spacing figure is possible. All stipes are clearly compound with bundles of elongate thecae.

**Remarks.** Koremagraptus pseudoplexus Bouček, 1957 from the Wenlock of Bohemia is one of the closest forms, having a similar pattern of stipes, but it is less robust than *K. elegantulus* and has frequent dissepiment-like branch connections which *K. elegantulus* lacks.

# Order Tuboidea Kozlowski, 1938 Family Tubidendridae Kozlowski, 1949 *Reticulograptus* Wiman, 1901

**Type species**. *Dictyonema tuberosum* Wiman, 1895, by original designation.

### Reticulograptus thomasi n.sp.

Figs. 22E, 23

**Material**. HOLOTYPE AM F114756, only specimen, from BF28, W tributary of Bridge Creek.

**Derivation of name**. After the late Dr D.E. Thomas, Australian biostratigrapher and graptolite authority.

**Diagnosis**. *Reticulograptus* with striking polygonal arrangement of stipe interspaces; only autothecae and possible bithecae have been identified, with no clustering of thecae into twigs, or even single autothecal terminations; no association of autothecae and bithecae,

**Description**. The only rhabdosomal fragment is exquisitely preserved with many individual autothecal tubes visible. Each stipe is effectively zig-zag and connections with adjacent stipes are exclusively transfers of autothecal tubes. Autothecal apertures are sometimes associated with the transfer from an adjacent stipe, with an autotheca opening just before or just after the point where the "arriving" theca reaches its new stipe position. Some smaller tubes may be bithecae, as at the extreme left of Fig. 22E. Autothecae and the possible bithecae open close to the stipe surface. Autothecal tubes have an average diameter of about 0.10 mm and the possible bithecae 0.05 mm. Stipe width is 0.20-0.35 mm. Stipes are compound with several elongate tubes comprising any one part of them. Branching gives an overall divergent pattern, and the interspaces are polygonal. Stipe spacing is 8 in 10 mm. Strictly speaking there are no dissepiments but the connecting bars of autothecal tubes are also spaced at about 8 in 10 mm.

**Remarks**. *Reticulograptus thomasi* n.sp. is a unique reticulograptid in its striking polygonal arrangement of stipe interspaces, although all the other biocharacters are typically reticulograptid. Only autothecae and possible bithecae have been identified, but there is no clustering of these into twigs, or even single autothecal terminations, and no association of autothecae and bithecae, all of which suggest this is a tuboid rather than a dendroid.

# Family Idiotubidae Kozlowski, 1949 *Cyclograptus* Spencer, 1884

**Type species.** *Cyclograptus rotadentatus* Spencer, 1884, p. 42; by original designation.

Remarks. Bulman (1970) referred to the branching of stipes at their mid-length in his revised diagnosis of the genus. However, the original material is not quite so consistent as this, as pointed out by Bouček (1957) who recorded much longer stipes in some species than in the type species. In Bouček's species (*C. irregularis* and *C. multithecatus*) and *C. scharyanus* (Göppert, 1860) the stipes divide at roughly mid-length, but with additional bifurcations occurring. Bouček (1957: p. 141) also questioned whether, given such long stipes, all the autothecae must originate in the thecorhiza: it seems unlikely.

# Cyclograptus? australis n.sp.

Fig. 21B

Material. HOLOTYPE AM F114651, from BF28, Bridge Creek.

**Derivation of name**. To record the possible occurrence of the genus in Australia.

**Diagnosis.** Cyclograptus? with thecorhiza; 32 peripheral stipes some 6 mm from thecorhiza; autothecal apertural regions clearly isolated; autothecal diameter 0.15 mm and spacing approximately 18–20 in 10 mm; bithecae possibly present as thin tubes in thecorhiza.

**Description.** The single rhabdosome has a "basal disc" or the corhiza 7 mm wide, possibly incomplete, from which about ten stipes arise. These bifurcate quite quickly, and then divide again in some cases, resulting in 32 peripheral

stipes some 6 mm from the thecorhiza. The rhabdosome appears to be incomplete although its general shape is clear. The stipes consist of bundles of long thecal tubes, and in several places the autothecae can be seen opening in isolated fashion, sometimes slightly bent ventrally. Their diameter is 0.15 mm and the autothecal spacing approximately 18–20 in 10 mm. The autothecal apertures appear to be unadorned by processes or spines except, possibly, a slight extension of the ventral lip. Long thecal tubes can be detected in both the thecorhiza and in the up-growing stipes, but the termination of the stipes is usually by a single ventrally-curved autotheca. Bithecae may be present as thin tubes in the thecorhiza but this is not certain. The stipes may be unbranched, may branch after one third of their length, occasionally after two thirds of their length, and two stipes branch three times.

**Remarks**. The thecae are unknown in any described species of Cyclograptus, other than as bundles of elongate tubes in the thecorhiza and stipe. In C.? australis n.sp. the autothecal apertural regions are clearly isolated. The type species, C. rotadentatus, also exhibits stipes terminating in a single autotheca, but is more regular in its branching than C.? australis. Cyclograptus scharyanus (Göppert, 1860) has a stem-like structure, unlike other cyclograptids. Cyclograptus irregularis Bouček, 1957 is a much more robust species with broad stipes, and C. multithecatus Bouček, 1957 has more compound stipes than C.? australis. All previously described species of Cyclograptus are Wenlock (Silurian) whereas our specimen is late Llandovery. The presence of a theorhiza in C.? australis with masses of thecal tubes, suggest the tuboid Cyclograptus but the stipe branching pattern seems greater than in other cyclograptids except perhaps C. multithecatus.

ACKNOWLEDGMENTS. We are most indebted to Dr Chris Jenkins for making available his collections and maps, and for discussing this project with us at various times. Graptolite collections made by Drs Jenkins and Warris were borrowed from the School of Geosciences, University of Sydney with much-appreciated assistance from Dr Tom Hubble. Property owners in the Four Mile Creek area, particularly Ken Williams of "Ashburnia", Tim Christofferson of "Avon Lea", David Hughes of "Glendalough" and Sinclair Stratton of "Ulah" have most graciously allowed free access to their properties and given guidance and assistance. Dr Ian Percival and Ms Lucy Muir are thanked for their assistance in the field in November, 2000. R.B.R. would like to record his thanks for financial support to Emmanuel College, Cambridge, the Department of Earth Sciences, Cambridge (Cowper Reed Fund Managers), the Royal Society, and the University of Cambridge. A.J.W. records his sincere gratitude for support by: the School of Geosciences and the SERC research group, University of Wollongong; the Betty Mayne research fund, administered by the Linnean Society of NSW: and Emmanuel College, Cambridge for the award of a Quartecentenary Visiting Fellowship during Lent Term, 2001. GHP collected in the 1950s and 1960s with financial assistance from the Department of Geology and Geophysics, University of Sydney.

### References

- Bassler, R., 1909. Dendroid graptolites of the Niagaran dolomites at Hamilton Ontario. *United States National Museum, Bulletin* 65: 1–76.
- Booker, F.W., 1950. The Angellong alluvial deep lead. *Annual Reports of the New South Wales Department of Mines (Geological Survey)*, 1939–1945: 24.
- Bouček, B., 1957. The dendroid graptolites of the Silurian of Bohemia. *Ústredniho Ústavu Geologicky Rozpravy* 23: 1–294.
- Bronn, H.G., 1849. *Index Palaeontologicus B, Enumerator Palaeontologicus*. Stuttgart: E. Schweizerbart'sche, 980 pp.
- Bull, E.E., 1987. Upper Llandovery Dendroid Graptolites from the Pentland Hills, Scotland. *Palaeontology* 30: 117–140.
- Bulman, O.M.B., 1927. Koremagraptus, a new Dendroid Graptolite. *Annals and Magazine of Natural History* 19: 344–347.
- Bulman, O.M.B., 1927–1967. A Monograph of the British Dendroid Graptolites, parts I–IV. *Palaeontographical Society Monographs*, i–ixiv, 1–97.
- Bulman, O.M.B., 1933. On the graptolites prepared by Holm. 6: Structural characters of some Dictyonema and Desmograptus species. *Arkiv für Zoologi* 26A: 1–52.
- Bulman, O.M.B., 1938. *Graptolithina*. In *Handbuch der Paläozoologie*, ed. O.H. Schindewolf, 2D, pp. 1–92.
- Bulman, O.M.B., 1970. Graptolithina with sections on Enteropneusta and Pterobranchia. In *Treatise on Invertebrate Paleontology*, ed. C. Teichert, pt. V, (2nd edition), i-xxxii+1-163
- Bulman, O.M.B., & R.B. Rickards, 1966. A revision of Wiman's Dendroid and Tuboid Graptolites. *Bulletin of the Geological Institutions of the University of Uppsala* 43: 1–72.
- Carne, J.E., & L.J. Jones, 1919. The limestone deposits of New South Wales. *Mineral Resources* 25. New South Wales Department of Mines, Geological Survey. Sydney: William Applegate Gullick, Government Printer, xii+411 pp.
- Chapman, A.J., P.N. Durman & R.B. Rickards, 1996. A provisional classification of the graptolite Order Dendroidea. *Paläontologische Zeitschrift* 70: 189–202.
- Chapman, A.J., & R.B. Rickards, 1982. Peridermal (cortical) ultrastructure in Dictyonema cf. rhinanthiforms Bulman, and the significance of its bithecae. *Paläontologische Zeitschrift* 56: 217–227.
- Chapman, A.J., R.B. Rickards & R. Grayson, 1993. The Carboniferous dendroid graptolites of Britain and Ireland. *Proceedings of the Yorkshire Geological Society* 49: 295–319.
- Frech, F., 1897. *Lethaea geognostica; Teil I, Lethaea palaeozoica, 1 Band, Graptolithiden* (Leif. 1–2 by Ferdinand Roemer; Leif. 3 by F. Frech), pp. 544–684, Stuttgart, E. Schweiz–erbart'sche.
- Göppert, H.R., 1860. Ueber die fossile Flora der Silurischen, der Devonischen und unteren Kohlen Formation oder des sogenannten Uebergangs Gebirges. Nova Acta Academiae Caesarae Lepoldino Carolinae Germanicae Naturae Curiosorum 27: 426-606.
- Gurley, R.R., 1896. North American graptolites. *Journal of Geology* 4: 63–102, 291–311.
- Hall, J., 1843. Geology of New York, IV, Survey of the Fourth Geological District. Natural History of New York. Geology of New York, 156 pp.
- Hall, J., 1851. New genera of fossil corals. *American Journal of Science* 11: 398–401.
- Hall, J., 1858. Descriptions of Canadian Graptolites. *Geological Survey of Canada, Report for 1857*: 111–145.
- Hall, J., 1862. New species of fossils from the investigations of the Survey. *Wisconsin Geological Survey, Report for 1861*: 1–18.
- Hall, J., 1865. Graptolites of the Quebec Group. Figures and descriptions of Canadian Organic remains. Dec. II, Canadian Geological Survey: 1–151.
- Holm, G., 1890. Gotlands Graptoliter. *Handlingar Kungliga Svenska Vetenskapakademiens* 16: 1–34.

- Hopkinson, J., & C. Lapworth, 1875. Description of the graptolites of the Arenig and Llandeilo of St David's. *Quarterly Journal of* the Geological Society of London 31: 631–672.
- Jenkins, C.J., 1973. Silurian biostratigraphy of the Four Mile Creek and "Angullong" area, central western N.S.W. Unpublished BSc (Hons) thesis, University of Sydney, 139 pp.
- Jenkins, C.J., 1978. Llandovery and Wenlock stratigraphy of the Panuara area, central New South Wales. Proceedings of the Linnean Society of New South Wales 102: 109–130.
- Jenkins, C.J., (compiler), 1986. *The Silurian of mainland Australia: a field guide*. IUGS Silurian Subcommission, University of Sydney, Sydney, 82 pp.
- Johnson, M.E., D. Kaljo & J.-Y. Rong, 1991. Silurian eustasy. *Special Papers in Palaeontology* 44: 145–163.
- Johnson, M.E., & W.S. McKerrow, 1991. Sea level and faunal changes during the latest Llandovery and earliest Ludlow. *Historical Biology* 5: 153–169.
- Kozlowski, R., 1938. Informations préliminaires sur les Graptolithes du Tremadoc de la Pologne et sur leur portée Théorique. Annales Musei Zoologie Polonica 13: 183–196.
- Kozlowski, R., 1949. Les graptolithes et quelques nouveaux groups d'animaux du Tremadoc de la Pologne. *Palaeontologica Polonica* 3: 1–235.
- Kraft, J., 1979. Dendroid graptolites of Llandoverian age from Hýskov near Beroun (Barrandian). Sborník geologickych Ved, Paleontologie 25: 83–95.
- Kraft, J., 1984. A new find of *Dendrograptus attenuatus* Bouček (Graptolithina, Dendroidea). Časopis pro mineralogii a geologii 29: 405–406.
- Lapworth, C., 1881. On the Cladophora (Hopk) or dendroid graptolites collected by Prof. Keeping in the Llandovery rocks of Mid Wales. Quarterly Journal of the Geological Society of London 37: 171–177.
- Miller, S.A., 1889. *North American geology and palaeontology*. Cincinnati, Ohio: Western Methodist Book Concern, 664 pp.
- Nicholson, H.A., 1872. *Monograph of British Graptolites*. Edinburgh & London: Blackwood & Sons, x+133 pp.
- Obut, A.M., & R.F. Sobolevskaya, 1966. Graptolity rannego silura v Kazakhstane. *Akademyia Nauk SSSR*, *Sibirskoe otdelenie, Institut Geologii ii Geofizikii*, pp. 1–56.
- Offenberg, A., 1963. *Geology of the Panuara-Cadia-Errowanbang area*, south of Orange, New South Wales. Unpublished BSc(Hons) thesis, University of Sydney, 112 pp.
- Packham, G.H., (compiler), 1969. The Geology of New South Wales. *Journal of the Geological Society of Australia* 16(1), 654 pp.
- Packham, G.H., I.G. Percival & G.C.O. Bischoff, 1999. Age constraints on strata enclosing the Cadia and Junction Reefs ore deposits of central New South Wales, and tectonic implications. *Quarterly Notes, Geological Survey of New South Wales* 110: 1–12.
- Packham, G.H., & N.C. Stevens, 1955. The Palaeozoic stratigraphy of Spring and Quarry Creeks, west of Orange, N.S.W. Journal and Proceedings of the Royal Society of New South Wales 88: 55–60
- Počta, P., 1894. Systême Silurien du Centre de la Bohême, 8, part 1, Bryozaires, Hydrozaires et partie des Athozaires. Prague, 230 pp.
- Pogson, D., & J.J. Watkins, 1998. Bathurst 1:250 000 Geological Sheet S/55–8: Explanatory Notes. Sydney: Geological Survey of New South Wales, 430 pp.
- Prout, A.H., 1851 Description of a new graptolite found in the Lower Silurian rocks near the Falls of St. Croix River. *American Journal of Science* 11: 187–191.
- Rickards, R.B., M.A. Hamedi & A.J. Wright, 1994. A new Arenig (Ordovician) graptolite fauna from the Kerman district, east-central Iran. *Geological Magazine* 131: 35–42.
- Rickards, R.B., M.A. Hamedi & A.J. Wright, 2001. New assemblages of graptolites, rhabdopleuran hemichordates and chitinous hydroids from the Arenig (Ordovician) of the Banestan area, Iran. *Alcheringa* 25: 169–190.

- Rickards, R.B., G.H. Packham, A.J. Wright & P.L. Williamson, 1995. Wenlock and Ludlow graptolite faunas and biostratigraphy of the Quarry Creek district, New South Wales. *Association of Australasian Palaeontologists, Memoir* 17: 1–68.
- Rickards, R.B., I.G. Percival, A.J. Simpson & A.J. Wright, 2001. Silurian biostratigraphy of the Cadia area, near Orange, New South Wales. *Proceedings of the Linnean Society of New South Wales* 123: 173–191.
- Rickards, R.B., & A.J. Wright, 1997. Graptolite zonation of the late Wenlock, with a new graptolite-brachiopod fauna from New South Wales. *Records of the Australian Museum* 49(3): 229–248.
- Rickards, R.B., & A.J. Wright, 1999. Systematics, biostratigraphy and evolution of the late Ludlow and Přídolí (Late Silurian) graptolites of the Yass district, New South Wales. Records of the Australian Museum 51(3): 187–215. http://www.amonline.net.au/pdf/publications/1306\_complete.pdf
- Roemer, F., 1897. (See under Frech, 1897).
- Ruedemann, R., 1905. Graptolites of New York. Part 1. Graptolites of the Lower beds. *New York State Museum, Memoir* 7: 457–803.
- Ruedemann, R., 1925. The Utica and Lorraine Formations of New York. I. Stratigraphy. *New York State Museum, Bulletin* 258: 1–175.
- Ruedemann, R., 1947. Graptolites of North America. *Geological Society of America Memoir* 19: 1–652.
- Sherrard, K.M., 1954. The assemblages of graptolites in New South Wales. *Journal and Proceedings of the Royal Society of New South Wales* 87: 73–101.
- Sherrard, K.M., 1956. Some dendroid graptolites from New South Wales. *Journal and Proceedings of the Linnean Society of New South Wales* 81: 82–90.
- Sherwin, L., 1971. Stratigraphy of the Cheesemans Creek district, New South Wales. Records of the Geological Survey of New South Wales 13: 199–237.
- Shrock, R., 1928. A new graptolite fauna from the Niagaran of northern Indiana. *American Journal of Science* 16: 1–38.
- Skevington, D., 1963. Graptolites from the Ontikan Limestones (Ordovician) of Öland, Sweden: I Dendroidea, Tuboidea, Camaroidea and Stolonoidea. *Bulletin of the Geological Institutes of the University of Uppsala* 42: 1–62.
- Spencer, J.W., 1878. Graptolites of the Niagara Formation. *Canadian Naturalist* 8: 457–463.
- Spencer, J.W., 1884. Graptolites of the Upper Silurian System. *University of Missouri Museum Bulletin* 1: 1–43.
- Stevens, N.C., & G.H. Packham, 1953. Graptolite zones and associated stratigraphy at Four Mile Creek, southwest of Orange, N.S.W. Journal and Proceedings of the Royal Society of New South Wales 86: 94–99.
- Warris, B.J.S., 1964. Some aspects of the stratigraphy and palaeontology of the Silurian syncline just west of "Angullong", Orange. Unpublished BSc (Hons) thesis, University of Sydney, Sydney.
- Wiman, C., 1895. Über die Graptolithen. *Bulletin of the Geological Institutes of the University of Uppsala* 2: 239–316.
- Wiman, C., 1901. Über die Borkholmer Schicht im Mittelbaltischen Silurgebiet. *Bulletin of the Geological Institutes of the University of Uppsala* 5: 149–222.

Manuscript received 27 November 2001, revised 11 October 2002 and accepted 28 November 2002.

Associate Editor: G.D. Edgecombe.

# The Triassic Amphibian *Thoosuchus yakovlevi* and the Relationships of the Trematosauroidea (Temnospondyli: Stereospondyli)

ROSS J. DAMIANI<sup>1\*</sup> AND ADAM M. YATES<sup>2</sup>

<sup>1</sup> Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa damianir@geosciences.wits.ac.za

<sup>2</sup> Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, United Kingdom adam\_m\_yates@yahoo.co.uk

ABSTRACT. A skull of the basal trematosauroid temnospondyl *Thoosuchus yakovlevi* from the Early Triassic of Russia is described. Characters showing phylogenetic affinities with the Trematosauroidea include the presence of a postorbital-prepineal growth zone, the well-developed sensory sulci, the ventrally knife-edged cultriform process of the parasphenoid, and the posteriorly expanded parasphenoid body. A preliminary phylogenetic analysis of trematosauroid relationships confirms that *Benthosuchus* is a basal trematosaurian rather than a basal mastodonsauroid, and that *Thoosuchus* is the sister group to all other trematosauroids. Relationships within the Trematosauroidea are poorly established with as yet little evidence for subdivision of the group as previously proposed. In addition, the hypothesis that the Metoposauroidea is nested within the Trematosauroidea is supported. However, the Trematosauridae *sensu stricto* appears to be paraphyletic. The basal stereospondyl dichotomy between the Mastodonsauroidea and its relatives (the Capitosauria), and the Trematosauroidea and its relatives (the Trematosauria), is supported, and now seems well established.

DAMIANI, ROSS J., & ADAM M. YATES, 2003. The Triassic amphibian *Thoosuchus yakovlevi* and the relationships of the Trematosauroidea (Temnospondyli: Stereospondyli). *Records of the Australian Museum* 55(3): 331–342.

The Trematosauridae is a diverse and cosmopolitan group of temnospondyl amphibians known from the Early, Middle and Late Triassic, and from all continents except South America and Antarctica. A review of the fossil record of trematosaurids can be found in Schoch & Milner (2000). Typical trematosaurids are distinctive in possessing narrow, moderately to highly elongated snouts with large palatal fangs, paired anterior palatal vacuities, an expanded postorbital-prepineal growth zone, a knife-edged cultriform process of the parasphenoid, an elongated basicranium, and a ventrally underplated exoccipital. The Trematosauridae is traditionally subdivided into two or three taxonomic groups, the highly-derived long-snouted Lonchorhynch-

inae, which make their first appearance in the earliest Triassic, and the short-snouted Trematosaurinae and Lyrocephalinae, which appear later in the Early Triassic (Säve-Söderbergh, 1935; Cosgriff & Garbutt, 1972; Hammer, 1987; Welles, 1993). Although most trematosaurids are easily recognizable as either lonchorhynchine or trematosaurine/lyrocephaline, the relationship between these subgroups is unclear because of their morphological disparity, the temporal gap, and the fact that the apparently more primitive taxa appear later in the fossil record. This has led to suggestions that the Trematosauridae may be diphyletic in origin (Bystrow & Efremov, 1940; Shishkin, 1964; Welles, 1993). Hence, this subdivision may simply

represent a convenient morphology-based grouping.

The origin of the Trematosauridae has been linked to a number of primitive, trematosaurid-like temnospondyls from the Early Triassic of Russia, the most widely cited of which are Benthosuchus (Bystrow & Efremov, 1940) and Thoosuchus (Riabinin, 1926). These genera are usually grouped together in the higher-level taxon Benthosuchidae (Efremov, 1940), which is thus considered by some workers (Hartmann-Weinberg & Kuzmin, 1936; Efremov, 1940; Shishkin, 1964, 1980; Getmanov, 1982, 1989; Shishkin & Welman, 1994) to include the ancestors of the Trematosauridae. Cladistic support for this hypothesis was first provided by Milner (1990), in his insightful hand-drawn phylogeny of temnospondyls. In that phylogeny, a more restricted Thoosuchidae (=Thoosuchinae of Getmanov, 1982) formed the paraphyletic stem group of a clade consisting of the Trematosauridae, Latiscopidae and Metoposauridae, and the Benthosuchidae (=Benthosuchinae of Getmanov, 1982) was placed in a more basal position within the phylogeny. In marked contrast, other workers (Romer, 1947; Morales & Kamphausen, 1984; Kamphausen, 1989) consider the Benthosuchidae (sensu lato) to be more closely related to the Mastodonsauroidea (the senior synonym of the more widely known Capitosauroidea: Damiani, 2001a). Warren & Black (1985) allied the Trematosauridae with the Rhytidosteidae in a monophyletic Trematosauroidea, which they considered far removed from the Benthosuchidae and "Capitosauridae". This hypothesis was adopted by Hammer (1987). None of the above hypotheses, however, were based on analyses of a data matrix.

The recent computer-based parsimony analyses of Yates & Warren (2000) and Damiani (2001a) found Thoosuchus to be the sister-taxon to the Trematosauridae in a monophyletic Trematosauroidea, whereas Benthosuchus was found to be more closely related to the Mastodonsauridae. Thus Thoosuchus and Benthosuchus were found to be only distantly related within the Stereospondyli (sensu Yates & Warren, 2000), and their phenetic similarity as due to their relatively plesiomorphic nature. However, the relationships within the Trematosauridae were not tested in either analysis, and in the analysis of Damiani (2001a) the Mastodonsauroidea was the sister-taxon to the Trematosauroidea, whereas in Yates & Warren (2000) the latter were more closely related to a clade consisting of the Metoposauroidea, Plagiosauroidea, Rhytidosteidae and Brachyopoidea. Interestingly, the problematic *Luzocephalus* (Shishkin, 1980), which was not included in Damiani's (2001a) analysis, was the sister-taxon to the *Thoosuchus*-Trematosauridae dichotomy in Yates & Warren (2000).

In the computer-based analysis of Schoch (2000), the basal trematosauroids *Benthosuchus* and *Thoosuchus* formed successive stem-taxa to the trematosaurids, which also included *Wetlugasaurus* as the most basal stem-trematosauroid, while the Trematosauroidea was found to be the sister-taxon to the Mastodonsauroidea, contra Yates & Warren (2000). This same hypothesis of relationships was proposed in the hand-crafted phylogeny of Schoch & Milner (2000), but in addition the Metoposauroidea was nested deeply within the Trematosauroidea; the latter consisted of two monophyletic groupings: the Trematosauridae *sensu stricto* (Trematosaurinae, Lonchorhynchinae and Tertreminae), and a large clade consisting of the Platystegidae, Lyrocephaliscidae, Almasauridae and Metoposauridae as successively more derived groups.

Finally, Steyer's (2002) computer-based analysis of trematosaurid intrarelationships found support for a monophyletic Trematosauridae consisting of the subgroups Trematosaurinae and Lonchorhynchinae, with *Watsonisuchus* (sensu Damiani, 2001a) and *Benthosuchus* forming successive stem-taxa to the Trematosauridae. The Metoposauroidea fell well outside of the trematosaurid clade, whereas *Luzocephalus* was found to be nested within the Trematosaurinae.

It is apparent that the phylogeny of trematosaurids remains contentious, but only the analysis of Stever (2002) has addressed the problem by means of parsimony analysis of a data matrix. Recently, we examined two superb skulls of the trematosauroid *Thoosuchus yakovlevi*, providing the stimulus for a broad cladistic analysis of trematosauroid relationships. Thus, the aims of this paper are to investigate basal trematosaurid phylogeny, determine the broad-scale relationships within the Trematosauridae (i.e. the basal branching events), and determine how the Trematosauridae is related, in the broadest sense, to other stereospondyls. We emphasize that our analysis is preliminary due to the poorly known nature of many trematosaurids; redescriptions of much of this material are currently being undertaken by Lindemann, Sengupta, Steyer, and the senior author, and will provide sorely needed data for future, more detailed cladistic studies. As a number of descriptions of the skull of T. yakovlevi are available in the literature (Riabinin, 1926; Hartmann-Weinberg & Kuzmin, 1936; Efremov, 1940; Getmanov, 1989), here we emphasize only characters of phylogenetic significance as a prelude to our phylogenetic analysis.

### Materials and methods

The specimens of *Thoosuchus yakovlevi* used in this study, AM F98271 and WAM 96.8.1, were purchased from a commercial fossil dealer in Melbourne, Australia, by the Australian Museum and the Western Australian Museum, respectively, and subsequently made available to us for study. These specimens were bought with the knowledge of the Palaeontological Institute, Moscow, and were not amongst the temnospondyl specimens stolen from that institution (Shishkin, 1992). Little is known as regards the history of the specimens except that labels associated with both indicate that they came from the Tikhvinskoye locality (Novikov & Sennikov, 1995) on the north bank of the Volga River near the city of Rybinsk, Yaroslavl Province, Russia. This locality has yielded dozens of three-dimensionally preserved skulls of T. yakovlevi, most of which are housed in the Palaeontological Institute, Moscow (Getmanov, 1989). All of the known species of *Thoosuchus* (Getmanov, 1989) come from the Rybinskian Horizon of the Vetluga Series of European Russia, of late Early Triassic (Lower Olenekian) age (Ivakhnenko et al., 1997).

The description below is based exclusively (unless otherwise stated) on AM F98271, an excellently preserved, distortion-free skull. However, the anteriormost region of the snout, a small section of the right palatine ramus of the pterygoid, a section of the left maxillary tooth row, and the tip of the left tabular horn are missing. In addition, the right posterolateral region of the skull roof, including most of the right tabular horn, is not preserved but has been cleverly reconstructed in plaster. AM F98271 was preserved in a fine-grained sandstone matrix. Details of the

endocranium are therefore gleaned from WAM 96.8.1, which has been acid prepared.

In our phylogenetic analysis, we follow the methodology of phylogenetic taxonomy. Thus, higher-level taxon names referred to in the text are defined phylogenetically (i.e. in terms of ancestry) and lack Linnean rank.

Institutional abbreviations used in the text are as follows: AM, Australian Museum, Sydney; BMNH, Natural History Museum, London; NM, National Museum, Bloemfontein; NMV, Museum of Victoria, Melbourne; PIN, Palaeontological Institute, Moscow; SAM, South African Museum, Cape town; UCMP, University of California Museum of Paleontology, Berkeley; WAM, Western Australian Museum, Perth.

Anatomical abbreviations used in the text are as follows: apv, anterior palatal vacuity; ch, choana; cm, *crista muscularis* of the parasphenoid; co, *crista obliqua* of the pterygoid; ect, ectopterygoid; eo, exoccipital; f, frontal; fm, foramen magnum; fs, *fossa subrostralis media*; ht, hyoid tubercle; ic, infraorbital canal; j, jugal; jc, jugal canal; l, lacrimal; lp, lamellose process of the exoccipital; mx, maxilla; n, nasal; na, naris; oc, occipital canal; p, parietal; pal, palatine; pf, parietal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; pop, paroccipital process; pp, postparietal; pqf, paraquadrate foramen; prf, prefrontal; psp, parasphenoid; pt, pterygoid; ptf, posttemporal fenestra; q, quadrate; qj, quadratojugal; sc, supraorbital canal; smx, septomaxilla; sq, squamosal; st, supratemporal; t, tabular; tc, temporal canal.

### **Description**

The skull of *Thoosuchus yakovlevi* (Figs. 1, 2) is wedgeshaped in outline and somewhat narrower than in Benthosuchus (Bystrow & Efremov, 1940) or mastodonsauroids. The orbits are situated approximately one-third of the way back on the lateral margins of the skull; their margins are not everted or "raised". The nostrils are oval but are clearly less elongated than those in *Benthosuchus*. A well-developed otic notch is present posteriorly, but is not as deeply incized as the otic notch of mastodonsauroids.

Ornament on the skull roof (Figs. 1A, 2A) is of the normal pattern and distribution found in most Mesozoic stereospondyls, with an additional, albeit poorly defined, area of ridge-groove ornamentation between the orbits and the pineal. This pattern is most clearly seen on the parietals. Ridge-groove ornament in this area is characteristic of trematosaurids (Säve-Söderbergh, 1937) and is held to indicate a "zone of intensive growth" (Bystrow, 1935) on the skull.

The well-developed lateral line system is represented by near-continuous grooves for the infraorbital, supraorbital, jugular and temporal canals, as well as an occipital sulcus which runs across the posterior margin of the skull deck. An anterior sulcus is also normally present (Getmanov, 1989) but not preserved in AM F98271. The absence of an occipital sulcus in a specimen illustrated by Getmanov (1989) may indicate a degree of variability in the expression of this character. An occipital sulcus is also present in other trematosaurids including *Angusaurus* (Getmanov, 1989; Novikov, 1990), *Trematosaurus* (Säve-Söderbergh, 1937), *Wantzosaurus* (Steyer, 2002) and some specimens of *Benthosuchus* (Bystrow & Efremov, 1940; Getmanov, 1986). The infraorbital sulcus forms a step-shaped rather

than Z-shaped flexure on the lacrimal bone, as in *Angusaurus*. In *Trematosaurus brauni* (Säve-Söderbergh, 1937) and derived trematosaurids, the infraorbital canal forms a smooth, sigmoidal curve. As in trematosaurids and some mastodonsaurids (Schoch & Milner, 2000; Damiani, 2001a), the supraorbital sulcus enters the lacrimal bone.

The arrangement of the dermal roofing bones is well known from the literature and only a few points will be raised here. Posterior to each nasal a small, triangular, ornamented septomaxilla is present as part of the skull roof. Ornamented septomaxillae have also been reported in various trematosaurids including Angusaurus (Getmanov, 1989) and Trematosuchus (Shishkin & Welman, 1994) but not in Trematosaurus. In contrast, the septomaxilla of mastodonsaurids appears to be attached to the inside of the naris (Mukherjee & Sengupta, 1998). The tabular horns of Thoosuchus, like those of trematosaurids, are short and triangular in shape, and contrast with those of mastodonsaurids which are elongated and (usually) rounded distally. The postorbitals resemble those of trematosaurids in being elongated, with no indication of expansion ("hooking") along the posterolateral orbital margin as in mastodonsaurids (Damiani, 2001a). As in Benthosuchus, Angusaurus and *Trematosaurus*, the frontals are primitively (Damiani, 2001a) excluded from the orbital margins and the projection of the jugals is greater posterior to the orbits than anterior to them. In contrast, in mastodonsaurids the frontals enter the orbital margin and there is a markedly elongated preorbital projection of the jugal.

The palate (Figs. 1B, 2B) displays narrow, elongated interpterygoid vacuities and paired anterior palatal vacuities. Between the latter, a shallow, circular depression, the *fossa subrostralis media* (Shishkin & Welman, 1994), is present, but has not been illustrated previously. This character is found in trematosaurids, archegosaurids and various other temnospondyls.

The cultriform process of the parasphenoid is deep, narrow and "knife-edged" ventrally, and the corpus of the parasphenoid is elongated. The latter is a derived character (e.g., Damiani, 2001a) and also occurs in Angusaurus, trematosaurids, derived mastodonsaurids and most brachyopoids. Also conspicuous is the posterior spreading of the parasphenoid to partially cover the subotic processes of the exoccipitals. In trematosaurids, this spreading is complete so that the exoccipitals are completely hidden ventrally (Warren & Black, 1985). Weakly developed, posteromedially oriented crests, the crista musculari (Bystrow & Efremov, 1940), are present on the base of the corpus of the parasphenoid. These are mainly exposed ventrally and to a lesser extent on the side walls (i.e. subotic process) of the exoccipital, as in lydekkerinids (Shishkin et al., 1996). As in Benthosuchus, Angusaurus, Trematosaurus, and some basal mastodonsaurids (Damiani, 2001a), the vomers form long, posteriorly directed processes which underplate the anterior portion of the cultriform process of the parasphenoid. The long ectopterygoids are broadly exposed in the margin of the interpterygoid vacuities, as in Trematosaurus, Angusaurus, and trematosaurids but not Benthosuchus or mastodonsaurids (Damiani, 2001a).

The maxillary teeth are simple, conical, rounded at their bases, and increase gradually in size from posterior to anterior. Most of these remain embedded in matrix but there were at least 70 teeth on the left maxilla. A continuous

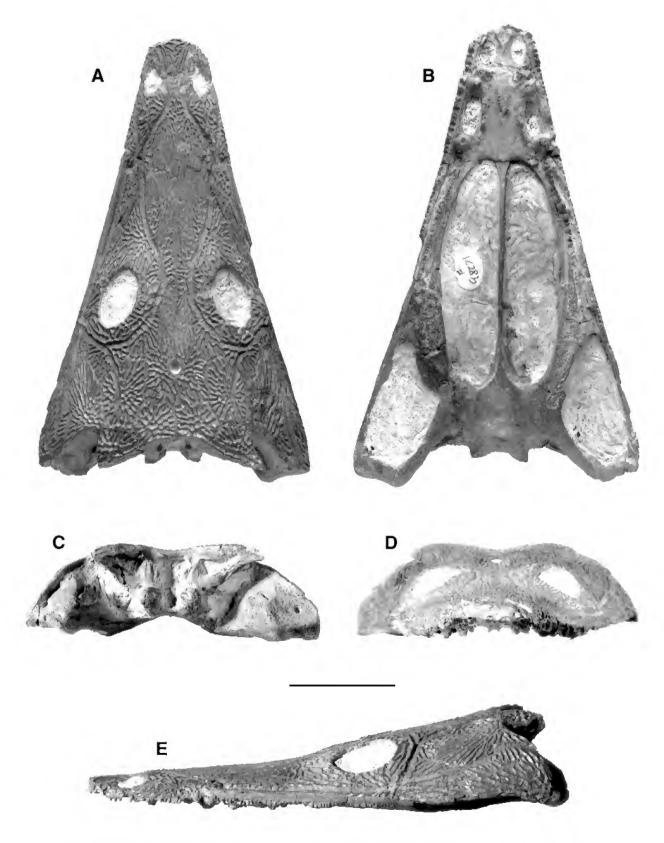
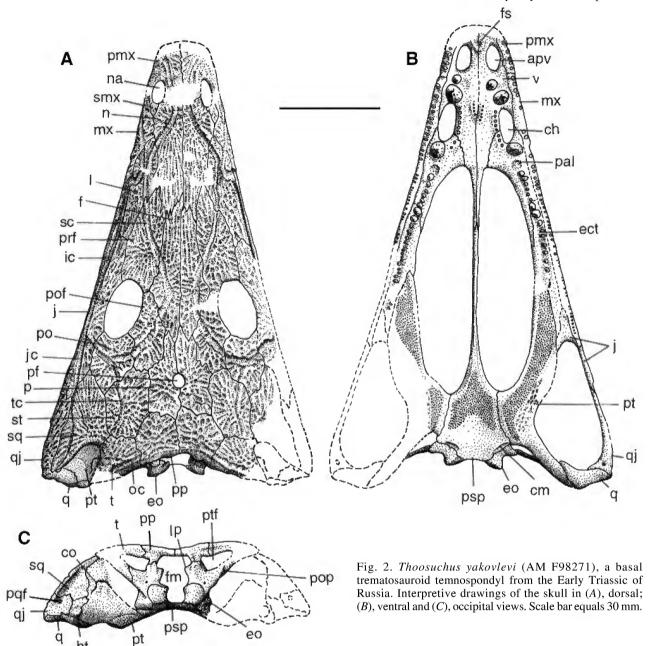


Fig. 1. *Thoosuchus yakovlevi* (AM F98271), a basal trematosauroid temnospondyl from the Early Triassic of Russia. Photographs of the skull in (A), dorsal; (B), ventral; (C), occipital; (D), anterior and (E), lateral views. Scale bar equals 30 mm.



tooth row and tusks are found on each of the vomers, palatines and ectopterygoids. The ectopterygoid tusks are poorly developed in AM F98271 and a small, presumably immature individual of this species (PIN 3200/279) lacks them altogether (Warren pers. comm.), suggesting late ontogenetic development of this character. Curiously, in the mastodonsaurids Watsonisuchus aliciae (Warren & Hutchinson, 1988; Warren & Schroeder, 1995) and Wellesaurus peabodyi (Welles & Cosgriff, 1965; RJD pers. obs.), ectopterygoid tusks are present in pre-adult but lost in adult individuals. A weakly developed, acutely V-shaped transvomerine tooth row is present well posterior to the anterior palatal vacuities. Conspicuous areas of denticles are present on the corpus of the parasphenoid and base of the cultriform process, and on the corpus and palatal ramus of the pterygoids. Small, faint patches of ornament are also present on the base of the corpus of the parasphenoid and on the pterygoids bordering the subtemporal vacuities.

In occipital view (Figs. 1C, 2C), the weakly developed crista obliqua of the pterygoid (Bystrow & Efremov, 1940) forms a very short, narrow lamina separated from the ascending ramus by a narrow slit. This differs from that of Benthosuchus (Getmanov, 1989) and Mastodonsaurids in which the lamina is tall and crest-like and borders a distinct channel. The occipital margin of the squamosal bears a short flange along most of its length which probably represents a reduced crista falciformis (Bystrow & Efremov, 1940). There is no palatoquadrate fissure in AM F98271, but one was illustrated in a specimen of T. yakovlevi by Getmanov (1989). However, the presence of this fissure may hinge on the degree of ossification and/or ontogeny. A palatoquadrate fissure is absent in Angusaurus (Getmanov, 1989), Trematosaurus (Watson, 1919), all other trematosaurids, and mastodonsaurids.

The ascending ramus of the pterygoid, visible in WAM 96.8.1 only, is nearly straight in dorsal view with only the

slightest hint of being recurved anteriorly. A moderate vertical thickening of its anterior margin represents the crista praeotica lamina ascendens (Getmanov, 1989), a structure thought to be present in all stereospondyls except *Lapillopsis* (Yates, 1999) and brachyopids (Damiani & Warren, 1996).

The ridges found on the ventral surface of the tabular horns in *Benthosuchus* (Bystrow & Efremov, 1940) and mastodonsaurids are not visible in *Thoosuchus* because the tips of both tabular horns are missing. As in all mastodonsaurids and *Trematosaurus* (Watson, 1919), the paroccipital processes bear a longitudinal *crista muscularis* along their posteroventral faces. A hyoid tubercle or quadrate "boss" is present on the occipital face of the quadrate near its suture with the pterygoid. This structure is present in *Benthosuchus* and mastodonsaurids but appears to be absent in trematosaurids.

### Phylogenetic analysis

**Methods**. The phylogenetic analysis presented here is intended to cover the diversity of putative stem-group trematosaurids, trematosaurines, and lonchorhynchines. Thus only select, well-known trematosaurid taxa have been used. The remaining terminals consist of a selection of genera and higher-level taxa that have been allied by one or more authors with some or all trematosaurids, as discussed in the Introduction. The 18 ingroup taxa, and the principal references used in coding the matrix, are as follows: the putative basal trematosaurids Benthosuchus (Bystrow & Efremov, 1940; Getmanov, 1989; RJD pers. obs. BMNH R7992), Thoosuchus (this paper) and Angusaurus (Getmanov, 1989), the trematosaurids Trematosaurus (Watson, 1919; Säve-Söderbergh, 1937; Schoch & Milner, 2000; RJD pers. obs. NMV P175723), Tertrema (Wiman, 1914; Säve-Söderbergh, 1936), Lyrocephaliscus (Säve-Söderbergh, 1936; Mazin & Janvier, 1983), Platystega (Säve-Söderbergh, 1936), Microposaurus (Haughton, 1925; RJD pers. obs. SAM-PK-6556), Aphaneramma (Säve-Söderbergh, 1935, 1936) and Cosgriffius (Welles, 1993), the mastodonsaurids Watsonisuchus (Warren, 1980; Damiani, 2001a; RJD pers. obs. NM QR3043), Wetlugasaurus (Sennikov, 1981; Schoch & Milner, 2000) and Parotosuchus (Damiani, 2001b), the almasaurid Almasaurus (Dutuit, 1976), the putative lydekkerinid Luzocephalus (Shishkin, 1980; Bjerring, 1999), and the higher-level taxa Metoposauridae, Lydekkerinidae and Rhytidosteidae, which were coded according to their bauplans. The data matrix (Table 1) was coded according to the adult (or presumed adult) condition for each character. A comprehensive list of references for the above taxa can be found in Schoch & Milner (2000). We have not included the Brachyopoidea in our analysis because their supposed closer relationship to the Mesozoic Stereospondyli than to Palaeozoic short-faced taxa is far from certain (e.g., Foreman, 1990; Milner, 1990; Damiani & Kitching, 2003; but see Yates & Warren, 2000 for a contrasting view). The outgroups used to determine character polarity are the Archegosauridae (Gubin, 1991, 1997) and the Rhinesuchidae (Watson, 1962). These higher-level taxa are widely considered to be successive outgroups to most or all of the Mesozoic stereospondyls (Milner, 1990; Schoch & Milner, 2000; Yates & Warren, 2000).

The analysis was based on 40 cranial characters (Table 2). Characters 5, 8, 10, 13, 16, 18, 22, 27, 29, 30 and 37 are multistate characters but only characters 5, 8, 13, 18 and 27 form clear transformation series and were thus ordered. All characters remained unweighted. Taxa having multiple states were treated as polymorphic. The data were analysed using the Heuristic search of PAUP 3.1.1 (Swofford, 1993) with the following settings: the tree-bisection-reconnection branch-swapping algorithm was used and trees obtained via the simple stepwise-addition sequence, zero-length branches were collapsed to yield polytomies, and all the shortest trees were kept. Characters were optimized under the Deltran algorithm.

Results and discussion. The analysis produced ten most parsimonious trees (MPTs) each of 109 steps, a consistency index of 0.523 and a retention index of 0.745. The composition of the Trematosauroidea is identical in these trees, varying only in the topology of the clade that includes *Aphaneramma, Cosgriffius, Platystega* and *Tertrema*. Figure 3A represents one of the ten MPTs chosen as our phylogenetic hypothesis on the basis of *a posteriori* assessment of character distribution. Nodes A through F on this cladogram are discussed below. A strict consensus of the ten trees, along with the decay index for each node, is shown in Figure 3B.

The broad-scale results of our phylogeny are in most ways consistent with recent phylogenetic hypotheses of stereospondyl relationships (Schoch & Milner, 2000; Yates & Warren, 2000). However, it differs markedly in the position of the Rhytidosteidae, which in those analyses is nested deeply within the Stereospondyli in a more derived position than the Capitosauria and Trematosauria. Here, the Rhytidosteidae is the sister-group to Luzocephalus (node B), as in the hypothesis of Milner (1990). This relationship is supported by two unambiguous synapomorphies: the absence of muscular pockets (crista musculari) on the ventral surface of the corpus of the parasphenoid (character 22, state 0), representing an apomorphic reversal, and the presence of a palatoquadrate fissure (character 33, state 1). The clade [Rhytidosteidae + Luzocephalus] is the sister-group to the Lydekkerinidae, a hypothesis broadly similar to that of Milner (1990) and Schoch & Milner (2000), but at odds with that of Yates & Warren (2000) who allied the Lydekkerinidae with the Mastodonsauroidea. This clade (node A) is supported by two unambiguous synapomorphies, the foreshortened snout (character 4, state 0) and the absence of a crista falciformis of the squamosal (character 10, state 0), and one ambiguous synapomorphy, the presence of a single anterior palatal vacuity (character 16, state 2), all representing apomorphic reversals. However, this clade is not robust and requires only one additional step to shift the Lydekkerinidae to various other basal positions within the Stereospondyli. Clearly, the position of the Lydekkerinidae within the Stereospondyli remains contentious. Similarly contentious is the affinities of Luzocephalus, which has elsewhere been allied with lydekkerinids (Shishkin et al., 1996; Schoch & Milner, 2000) or trematosaurids (Yates & Warren, 2000; Stever, 2002).

The remaining clade of "higher" stereospondyls (node C) consists of a sister-group relationship between the Capitosauria (node D) and the Trematosauria (node E), and

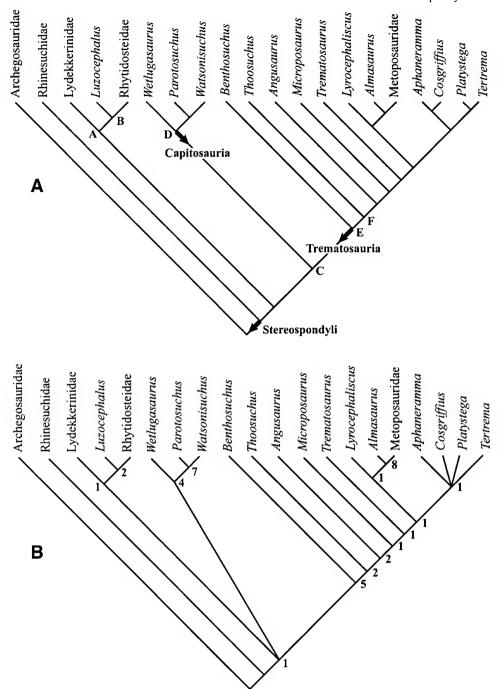


Fig. 3. Phylogeny of trematosauroid temnospondyls and related taxa resulting from a PAUP analysis of the data matrix presented in Table 1. (*A*), preferred phylogeny representing one of the ten most parsimonious trees (MPTs), showing the Capitosauria and Trematosauria (denoted by short arrows) as defined by Yates & Warren (2000). Nodes A–F discussed in the text. (*B*), strict consensus of ten MPTs, showing decay index for each clade.

is supported by one ambiguous synapomorphy, the step-shaped lacrimal flexure (character 13, state 1), and one unambiguous synapomorphy, the presence of teeth on the posterior coronoid only (character 37, state 1). A similar basal stereospondyl dichotomy between the Mastodon-sauridae (or Mastodonsauroidea in more inclusive analyses) and the Trematosauroidea was found by Schoch (2000), Schoch & Milner (2000), Yates & Warren (2000) and Damiani (2001a). Yates & Warren (2000) erected the terms Capitosauria and Trematosauria to refer to the Mastodon-sauroidea and its stem-group, and the Trematosauroidea

and its stem-group, respectively, and provided formal phylogenetic definitions for these taxa. Yates & Warren (2000) defined the Trematosauria as all stereospondyls sharing a more recent common ancestor with *Trematosaurus* than with *Parotosuchus*, and the Capitosauria as all stereospondyls sharing a more recent common ancestor with *Parotosuchus* than with *Siderops*. Under the latter definition, however, the composition of the Capitosauria can alter drastically depending upon the phylogenetic position of *Siderops* (Brachyopoidea) within temnospondyl phylogeny. If, as various authors have argued, the

Brachyopoidea do not form part of the Stereospondyli, then the Capitosauria could potentially include most of the Stereospondyli. Thus we advocate a slightly modified definition of the Capitosauria: All stereospondyls sharing a more recent common ancestor with *Parotosuchus* than with *Trematosaurus*. This definition remains relatively insensitive to large-scale shifts in the position of the Brachyopoidea while maintaining the integrity of the basal dichotomy between mastodonsauroids and trematosauroids. Although Schoch & Milner (2000) used the term Capitosauroidea" and Trematosauroidea, they did not define it phylogenetically.

In most previous hypotheses of mastodonsauroid relationships, Wetlugasaurus has been considered either a basal mastodonsaurid or a sister-group to them (e.g., Ochev, 1966; Ingavat & Janvier, 1981; Kamphausen, 1989; Milner, 1990; Maryanska & Shishkin, 1996; Damiani, 2001a). However, in the recent phylogenetic analyses of Schoch (2000) and Schoch & Milner (2000), Wetlugasaurus was considered the most basal stem-trematosauroid, with Benthosuchus and Thoosuchus forming successively more derived outgroups to the remaining trematosauroids. The synapomorphies used to support this arrangement are as follows (our numbering): (1) presence of a V-shaped transvomerine tooth row; (2) processus parasphenoidales of the vomers which conceal the cultriform process anteriorly; (3) narrow, elongated frontals, postfrontals and postorbitals: (4) small orbits located anterolaterally on the skull roof; (5) nostrils located medially on the snout which is elongated anterior to them. Of these, character (3) pertains only to trematosaurids in which a postorbital-prepineal growth zone has developed, a condition not met in Wetlugasaurus; character (4) does not pertain to Wetlugasaurus because its orbits are large and located within the posterior half of the skull roof; and character (5) does not pertain to Wetlugasaurus because its nostrils are located near the skull margins and the snout is not elongated anterior to them. Thus, the position of Wetlugasaurus in their analysis appears to hinge largely on characters (1) and (2) above. In contrast, our analysis supports the traditional hypothesis of inclusion of Wetlugasaurus in the Mastodonsauridae (node D). This clade requires four additional steps in order to make Wetlugasaurus the most basal stem-trematosauroid, and its monophyly is supported by one ambiguous synapomorphy, the presence of a single anterior palatal vacuity (character 16, state 2), representing an apomorphic reversal, and six unambiguous synapomorphies, the well-developed crista falciformis of the squamosal (character 10, state 2), the Z-shaped lacrimal flexure (character 13, state 2), the transversely expanded crista musculari of the parasphenoid (character 22, state 2), the strongly anteroposteriorly compressed tooth bases (character 28, state 1), the tall, crest-like oblique ridge of the pterygoid (character 34, state 2), and the well-developed hamate process of the prearticular (character 38, state 1). Nevertheless, we concede that the presence of characters (1) and (2) above, along with exclusion of the frontal from the orbital margin (a symplesiomorphy), are persuasive characters tying Wetlugasaurus to trematosauroids. Full resolution of this problem must await the discovery of additional fossils in the critical period prior to the initial radiation of the Mesozoic stereospondyls, an event which probably occurred in the latest Permian (Yates & Warren, 2000: Warren et al., 2000: Damiani, 2001a).

The hypothesis that the Trematosauridae may be diphyletic in origin (Shishkin, 1964; Welles, 1993) is not supported by our analysis, which recognizes only one monophyletic group (node E). *Benthosuchus, Thoosuchus* and *Angusaurus* form a series of stem-taxa of the remaining trematosauroids, as also found by Schoch (2000) and Schoch & Milner (2000). This clade (node E) is strongly

**Table 1.** Data matrix and character distribution. Character states are denoted by the following symbols: 0 = primitive; 1, 2, 3 = derived; ? = state unknown due to inadequate preservation; dash (-) = character inapplicable; P = polymorphic (states 0 and 1 present).

Characters	00000	00001	11111	11112	22222	22223	33333	33334
Taxa	12345	67890	12345	67890	12345	67890	12345	67890
Almasaurus	01100	00011	11010	31210	00110	12022	1100?	0201?
Angusaurus	11111	00010	01111	31200	10101	10012	10010	01010
Aphaneramma	11112	00010	01011	31100	10111	?2010	10110	0001?
Benthosuchus	10011	00111	01111	31100	11000	00012	11010	01000
Cosgriffius	11112	100??	?10 - ?	00??0	1????	??0?0	10???	?????
Luzocephalus	00000	00110	00000	21100	00000	00011	11110	1????
Lydekkerinidae	00000	00110	00100	20100	01000	00011	11010	10000
Lyrocephaliscus	11100	00010	01011	31200	10101	?1011	10120	0????
Metoposauridae	01100	00012	111-0	30211	01110	12021	11001	?0011
Microposaurus	01101	00010	010??	3?200	10101	20000	10???	0????
Parotosuchus	00010	01212	00200	20100	02000	00121	11020	01101
Platystega	01111	00010	0????	30200	10111	?1010	10???	?????
Rhytidosteidae	01000	10010	000-0	20-00	00000	00000	10100	00001
Tertrema	11111	00010	01010	30200	10111	?00?0	00???	?????
Thoosuchus	11111	00011	01111	31200	11100	00012	10010	01010
Trematosaurus	11101	00010	01011	31200	10111	?1010	10110	01010
Watsonisuchus	00010	01212	00200	20100	02000	00121	11020	01101
Wetlugasaurus	00010	00112	00200	21100	02000	00112	11020	01100
Archegosauridae	P0011	0000P	00000	30000	01000	0000P	01010	00000
Rhinesuchidae	00010	00101	00000	10P00	01000	00001	01010	00010

### Table 2. Characters and character states.

# Skull Roof

- 1 Skull outline in dorsal view: broad, rounded (0); narrow, wedge-shaped (1).
- 2 Position of orbits: medially displaced, approximately inline with nostrils (0); laterally displaced, close to margin of skull (1).
- 3 Postorbital-prepineal growth zone: absent (0); present (1). In the derived state the dermal sculpturing between the orbits and the pineal includes elongated ridges and grooves forming a "zone of intensive growth" (Bystrow, 1935); that is, where strong allometric growth has occurred.
- 4 Length of snout (i.e. preorbital portion of skull): less than 50% of total skull length (0); greater than 50% of total skull length (1). This character pertains to adult individuals only, as the shape of the skull in juvenile temnospondyls can differ significantly from that of adults (Boy & Sues, 2000).
- 5 Prenarial snout length: less than internarial distance (0); equals or exceeds internarial distance (1); greater than three times internarial distance (2).
- 6 Lacrimal: present (0); absent (1).
- 7 Frontal: excluded from medial margin of orbit by prefrontalpostfrontal suture (0); enters medial margin of orbit (1).
- 8 Postorbital: unexpanded anterolaterally (0); moderately expanded anterolaterally (1); strongly expanded anterolaterally (2).
- 9 Supratemporal: enters margin of otic notch (0); excluded from margin of otic notch by squamosal-tabular suture (1).
- 10 Crista falciformis of squamosal: absent (0); weakly developed, partially constricting otic notch posteriorly (1); well developed, strongly constricting otic notch posteriorly (2).
- 11 Well defined gutter surrounding otic notch: absent (0); present (1).
- 12 Lateral line sensory sulci: weakly impressed, discontinuous (0); well impressed, continuous (1).
- 13 Lacrimal flexure of the infraorbital sensory sulcus: absent (0); step-shaped (1); Z-shaped (2).
- 14 Supraorbital sensory sulcus: excluded from lacrimal (0); enters lacrimal (1).
- 15 Occipital sensory sulcus: absent (0); present (1).

### Palate

- 16 Anterior palatal "vacuity": absent (0); forming shallow fossa (1); single vacuity (2); paired or incipiently paired (i.e. bilobed) vacuities/foramina (3).
- 17 Processus parasphenoidales of the vomers: separated by median exposure of cultriform process of parasphenoid (0); meet in midline to conceal cultriform process anteriorly (1).
- 18 Contribution of palatine and ectopterygoid to margin of interpterygoid vacuity: both excluded by pterygoid-vomer contact (0); palatine only included (1); both palatine and ectopterygoid included (2). This character reflects a progressive retreat of the pterygoid from the lateral margins of the interpterygoid vacuities, and is therefore ordered.
- 19 Posteromedial expansion of ectopterygoid: absent (0); present, forms significant part of strut separating interpterygoid vacuity from subtemporal vacuity (1).

- 20 Distinct depression or foramen at anterior tip of cultriform process of the parasphenoid: absent (0); present (1).
- 21 Ventral surface of cultriform process of parasphenoid: simple, flattened bar (0); with midline, "knife-edged" keel (1).
- 22 Muscular pockets (*crista musculari*) on ventral surface of corpus of parasphenoid: absent (0); present, convex and widely spaced (1); present, transversely expanded so as to approach or merge in the midline (2).
- 23 Length of pterygoid-parasphenoid (basicranial) suture: shorter than width of parasphenoid body (0); longer than width of parasphenoid body (1).
- 24 Quadrate ramus of the pterygoid: long, posteriorly directed (0); short, posterolaterally or laterally directed (1).
- 25 Exoccipital: fully exposed ventrally (0); underplated by posterior extension of parasphenoid (1).
- 26 Ventral exoccipital-pterygoid suture: absent (0); present (1).
- 27 Position of exoccipital condyles relative to quadrate condyles: anterior to condyles (0); level or slightly posterior to condyles (1); well posterior to condyles (2).

### **Palatal Dentition**

- 28 Marginal dentition: circular to sub-circular at base (0); strongly anteroposteriorly compressed at base (1).
- 29 Palatal shagreen (denticles): extensive field throughout palate (0); localized patches (1); absent (2).
- 30 Tooth row on vomers posterior to anterior palatal vacuity: absent (0); transverse or arcuate (1); V-shaped or paired parallel rows (2).
- 31 Tooth row medial to choana: absent (0); present (1).
- 32 Ectopterygoid tusks: present (0); absent (1). This character pertains to adult individuals only, as ectopterygoid tusks are present in juvenile but not adult individuals of some species (e.g., "Parotosuchus" aliciae, Wellesaurus peabodyi) (Damiani 2001a).

### **Occiput**

- 33 Palatoquadrate fissure between cheek and palate: absent (0); present (1).
- 34 *Crista obliqua* on quadrate ramus of pterygoid: absent (0); low, rounded (1); tall, crest-like (2).
- 35 Post-temporal fenestrae: large, triangular (0); small, circular (1).
- 36 Cheek contour in occipital view: curved (0); straight (1).

### Mandible

- 37 Coronoid teeth: absent from all coronoids (0); present on posterior coronoid only (1); present on two or all three coronoids (2).
- Hamate process of the prearticular: absent or rudimentary (0); large, well developed (1).
- 39 Length of posterior meckelian foramen: less than (or equal to) 50% of length of adductor fossa (0); greater than 50% of length of adductor fossa (1).
- 40 Post-symphyseal tooth row: absent (0); present (1).

supported, requiring five additional steps to break, and is diagnosed by two ambiguous synapomorphies, the *processus parasphenoidales* of the vomers which conceal the cultriform process anteriorly (character 17, state 1) and V-shaped or paired parallel transvomerine teeth (character 30, state 2), and six unambiguous synapomorphies, the narrow, wedge-shaped skull (character 1, state 1), an elongated prenarial region (character 5, state 1), well impressed, continuous sensory sulci (character 12, state 1), the supraorbital sulcus entering the lacrimal (character 14, state 1), the presence of an occipital sulcus (character 15, state 1), and a knife-edged cultriform process (character 21, state 1).

We find little support for the hypothesis that Benthosuchus is the most basal mastodonsauroid (Yates & Warren, 2000; Damiani, 2001a), and feel that some of the synapomorphies used to support that hypothesis are unconvincing. These include, in Yates & Warren's (2000) analysis, the presence of a ventrally open supraglenoid foramen, which does not in fact occur in mastodonsaurids (Warren & Snell, 1991) and which is known to vary with ontogeny in some taxa (Schoch, 1999), and the absence of shagreen on the coronoid series, which also occurs in trematosaurids. In Damiani's (2001a) analysis, three of the six unambiguous synapomorphies used to support the same relationship are incorrectly coded for Benthosuchus; these are the presence of a step-shaped lacrimal flexure, strongly anteroposteriorly compressed tooth bases, and a tall, crestlike oblique ridge of the pterygoid. We are therefore inclined to regard Benthosuchus as a stem-trematosauroid, as indicated by our phylogeny.

Relationships within the Trematosauroidea are poorly established, with Microposaurus and Trematosaurus forming successive stem-taxa to a clade consisting of a sister-group relationship between Lyrocephaliscus plus the Metoposauroidea (sensu Yates & Warren, 2000: Metoposauridae + Almasaurus), and a clade consisting of Aphaneramma and Cosgriffius (lonchorhynchines), Platystega and Tertrema. Thus, our phylogeny supports that of Milner (1990) and Schoch & Milner (2000), but not that of Yates & Warren (2000) or Steyer (2002), in having the Metoposauroidea nested within the trematosauroids. As a consequence, the Trematosauridae, as usually conceived, appears to be paraphyletic according to our analysis. Furthermore, the monophyly of the traditional, more restricted Trematosauridae, as conceived by earlier workers (e.g., Säve-Söderbergh, 1935; Hammer, 1987) and supported by the analyses of Schoch & Milner (2000) and Stever (2002), could also not be supported. Thus, we see little evidence for the long-held basic subdivision of the trematosauroids into long-snouted lonchorhynchines and short-snouted trematosaurines, or of a finer subdivision into the categories of Hellrung (1987) or Schoch & Milner (2000). Note that in our analysis most of the clades within the Trematosauroidea are tenuous and require only one additional step to break, but no tree could be obtained which showed a monophyletic Trematosauridae. We conclude that relationships within the Trematosauroidea are poorly established, and that the Trematosauridae, as traditionally conceived, is not a clade. Resolution of these problems must await redescriptions of poorly known taxa and/or additional data.

A number of authors have used the name Trematosauroidea for the clade that includes *Benthosuchus* and which would coincide with node E in our analysis (Getmanov, 1989; Schoch & Milner, 2000). However, Yates & Warren (2000) defined the Trematosauroidea as the last common ancestor of *Thoosuchus* and *Trematosaurus* and all its descendants, corresponding to node F on our phylogeny. Thus *Benthosuchus* is excluded from the Trematosauroidea, but not from the Trematosauria (sensu Yates & Warren, 2000). This definition is favourable because, although we disagree with the hypothesis that *Benthosuchus* is closer to mastodonsaurids, it remains insensitive to potential changes in the position of *Benthosuchus*.

# Phylogenetic conclusions

Despite a number of recent phylogenetic analyses of stereospondyl relationships (Warren & Black, 1985; Milner, 1990; Schoch & Milner, 2000; Yates & Warren, 2000; Damiani, 2001a), it is apparent that much additional work remains before a consensus of relationships is reached. This concerns not only the broader relationships within the Stereospondyli, but also, as highlighted in our analysis of the Trematosauroidea, the relationships within particular groups.

The Trematosauroidea appears to be a well-defined group of stereospondyls within which are nested the Metoposauroidea. Consequently, the Trematosauridae, as traditionally perceived, appears to be paraphyletic. Thoosuchus is the most basal member of the Trematosauroidea as defined by Yates & Warren (2000), with Benthosuchus basal to them. Relationships within the Trematosauroidea are poorly established in our analysis, with little evidence for subdivision into lonchorhynchines and trematosaurines, or other proposed subgroups. The poor state of knowledge of many trematosaurids precludes a more detailed analysis and contributes to the low support (as indicated by decay indices) for many of the clades in our analysis. The Trematosauroidea and its relatives (the Trematosauria) share a common ancestry with the Mastodonsauroidea and its relatives (the Capitosauria), a basal stereospondyl dichotomy which now seems well established.

ACKNOWLEDGMENTS. We are indebted to Dr Anne Warren (La Trobe University, Melbourne) for her instrumental role in securing both AM F98271 and WAM 96.8.1 for the Australian Museum and Western Australian Museum, respectively. Mr Robert Jones (Australian Museum, Sydney) loaned us AM F98271, and Dr John Long (Western Australian Museum, Perth) allowed us to examine WAM 96.8.1. We are grateful to the following individuals for access to specimens held at their institutions: Dr Pat Holroyd, University of California Museum of Paleontology, Berkeley; Sandra Chapman, Natural History Museum, London; Dr Roger Smith, South African Museum, Cape Town; Dr Jenny Clack, University Museum of Zoology, Cambridge. Dr Sean Modesto (Carnegie Museum of Natural History, Pittsburgh) provided the inspiration for this paper and valuable comments on an earlier version of the manuscript. We also thank the referees, Drs Anne Warren and Sébastien Steyer, for valuable comments on the manuscript, and Dr Greg Edgecombe for editorial assistance.

### References

- Bjerring, H.C., 1999. A new amphibious tetrapod from the Greenlandic Eotriassic. *Meddelelser om Grønland, Geosciences* 38: 1–42.
- Boy, J.A., & H.-D. Sues, 2000. Branchiosaurs: larvae, metamorphosis and heterochrony in temnospondyls and seymouriamorphs. In *Amphibian Biology, Volume 4. Palaeontology, the evolutionary history of amphibians*, ed. H. Heatwole & R.L. Carroll, pp. 1150–1197. Chipping Norton: Surrey Beatty & Sons.
- Bystrow, A.P., 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Wirbeltiere. *Acta Zoologica* 16: 65–141.
- Bystrow, A.P., & J.A. Efremov, 1940. *Benthosuchus sushkini* Efremov—a labyrinthodont from the Eotriassic of the Sharzenga River. *Trudy Paleontologicheskogo Instituta* 10: 1–152. [In Russian]
- Damiani, R.J., 2001a. A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli, Stereospondyli). *Zoological Journal of the Linnean Society* 133: 379–482.
- Damiani, R.J., 2001b. *Parotosuchus* (Amphibia, Temnospondyli) from the *Cynognathus* Assemblage Zone (Early Triassic) of South Africa: cranial morphology and relationships. *Alcheringa* 25: 351–379.
- Damiani, R.J., & J.W. Kitching, 2003. A new brachyopid temnospondyl from the *Cynognathus* Assemblage Zone, Upper Beaufort Group, South Africa. *Journal of Vertebrate Paleontology* 23: 68–79.
- Damiani, R.J., & A.A. Warren, 1996. A new look at members of the Superfamily Brachyopoidea (Amphibia, Temnospondyli) from the Early Triassic of Queensland and a preliminary analysis of brachyopoid relationships. *Alcheringa* 20: 277–300.
- Dutuit, J.-M., 1976. Introduction à l'étude paléontologique du Trias Continental Marocain. Descriptions des premiers Stégocéphales receuillis dans le Couloir d'Argana (Atlas Occidental). Mémoires du Muséum National d'Histoire Naturelle, Paris 36: 1–253.
- Efremov, J.A., 1940. Preliminary description of the new Permian and Triassic Tetrapoda from U.S.S.R. *Trudy Paleontologicheskogo Instituta* 10: 1–140. [In Russian]
- Foreman, B.C., 1990. A revision of the cranial morphology of the Lower Permian temnospondyl amphibian *Acroplous vorax* Hotton. *Journal of Vertebrate Paleontology* 10: 390–397.
- Getmanov, S.N., 1982. A labyrinthodont from the Lower Triassic of the Obshchiy Syrt Region. *Paleontological Journal* 1982: 102–106
- Getmanov, S.N., 1986. On the individual variation of the skull in the benthosuchids as related to the development of the trematosaur in plan of organization. *Paleontological Journal* 1986: 76–85.

- Getmanov, S.N., 1989. Triassic amphibians of the East European platform (family Benthosuchidae Efremov). *Trudy Paleontologicheskogo Instituta* 236: 1–102. [In Russian]
- Gubin, Y.M., 1991. Permian archegosauroid amphibians of the USSR. *Trudy Paleontologicheskogo Instituta* 249: 1–141. [In Russian]
- Gubin, Y.M., 1997. Skull morphology of *Archegosaurus decheni* Goldfuss (Amphibia, Temnospondyli) from the Early Permian of Germany. *Alcheringa* 21: 103–121.
- Hammer, W.R., 1987. Paleoecology and phylogeny of the Trematosauridae. *American Geophysical Union, Geophysical Monograph Series* 41: 73–83.
- Hartmann-Weinberg, A., & F.M. Kuzmin, 1936. Untertriadische Stegocephalen der UdSSR *Lyrocephalus acutirostris* nov. sp. *Problems of Paleontology* 1: 63–84. [In German and Russian]
- Haughton, S.H., 1925. Investigations in South African fossil reptiles and Amphibia (Part 13). Annals of the South African Museum 22: 227–261.
- Hellrung, H., 1987. Revision von *Hyperokynodon keuperinus* Plieninger (Amphibia: Temnospondyli) aus dem Schilfsandstein von Heilbronn (Baden-Württemberg). *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie*) 136: 1–28.
- Ingavat, R., & P. Janvier, 1981. *Cyclotosaurus* cf. *posthumus* Fraas (Capitosauridae: Stereospondyli) from the Huai Hin Lat Formation (Upper Triassic), northeastern Thailand with a note on capitosaurid biogeography. *Géobios* 14: 711–725.
- Ivakhnenko, M.F., V.K. Golubev, Y.M. Gubin, N.N. Kalandadze, I.V. Novikov, A.G. Sennikov & A.S. Rautian, 1997. *Permian and Triassic tetrapods of Eastern Europe*. Moscow: GEOS. [In Russian]
- Kamphausen, D., 1989. Der Schädel von *Eocyclotosaurus* woschmidti Ortlam (Amphibia, Stegocephalia) aus dem Oberen Buntsandstein (Trias) des Schwarzwaldes (SW-Deutschland). Stuttgarter Beiträge zur Naturkunde Serie B 149: 1–65.
- Maryanska, T., & M.A. Shishkin, 1996. New cyclotosaurid (Amphibia, Temnospondyli) from the Middle Triassic of Poland and some problems of interrelationships of capitosauroids. *Prace Muzeum Ziemi* 43: 53–83.
- Mazin, J.-M., & P. Janvier, 1983. L'anatomie de Lyrocephaliscus euri (Wiman), Trématosaure du Trias Inférieur du Spitsberg: arrière-crâne, squalette axial et ceinture scapulaire. Palaeovertebrata 13: 13–31.
- Milner, A.R., 1990. The radiations of temnospondyl amphibians. *Systematics Association Special Volume* 42: 321–349.
- Morales, M., & D. Kamphausen, 1984. *Odenwaldia heidelbergensis*, a new benthosuchid stegocephalian from the Middle Buntsandstein of the Odenwald, Germany. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1984: 673–683.
- Mukherjee, R.N., & D.P. Sengupta, 1998. New capitosaurid amphibians from the Triassic Denwa Formation of the Satpura Gondwana Basin. *Alcheringa* 22: 317–327.
- Novikov, I.V., 1990. New Early Triassic labyrinthodonts from the Middle Timan. *Paleontological Journal* 1990: 48–60.
- Novikov, I.V., & A.G. Sennikov, 1995. A unique continental Lower Triassic vertebrate locality in the European part of Russia. *Journal of Vertebrate Paleontology* 15: 47A.
- Ochev, V.G., 1966. Systematics and phylogeny of capitosauroid labyrinthodonts. Saratov: Saratov State University Press. [In Russian]
- Riabinin, A.N., 1926. *Trematosuchus* (?) *yakovlevi* nov. sp. from the Lower Triassic deposits in the surroundings of Rybinsk. *Izvestiya Geologicheskago Komiteta* 45: 519–527. [In Russian]
- Romer, A.S., 1947. Review of the Labyrinthodontia. Bulletin of the Museum of Comparative Zoology, Harvard University 99: 1–352.
- Säve-Söderbergh, G., 1935. On the dermal bones of the head in labyrinthodont stegocephalians and primitive Reptilia with special reference to Eotriassic stegocephalians from East Greenland. *Meddelelser om Grønland* 98: 1–211.

- Säve-Söderbergh, G., 1936. On the morphology of Triassic stegocephalians from Spitzbergen and the interpretation of the endocranium in the Labyrinthodontia. *Kungliga Svenska Vetenskapsakademiens Handlingar (ser. 3)* 16: 1–181.
- Säve-Söderbergh, G., 1937. On the dermal skulls of *Lyrocephalus*, *Aphaneramma*, and *Benthosaurus*, labyrinthodonts from the Triassic of Spitsbergen and N. Russia. *Bulletin of the Geological Institution of the University of Uppsala* 27: 189–208.
- Schoch, R.R., 1999. Comparative osteology of *Mastodonsaurus giganteus* (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen). *Stuttgarter Beiträge zur Naturkunde Serie B* 278: 1–175.
- Schoch, R.R., 2000. The origin and intrarelationships of Triassic capitosaurid amphibians. *Palaeontology* 43: 705–727.
- Schoch, R.R., & A.R. Milner, 2000. *Stereospondyli*. Handbuch der Paläoherpetologie, Teil 3B. München: Verlag Dr. Friedrich Pfeil.
- Sennikov, A.G., 1981. A new wetlugasaur from the Samara River Basin. *Paleontological Journal* 1981: 111–116.
- Shishkin, M.A., 1964. Stereospondyli. In *Fundamentals of Palaeontology: amphibians, reptiles and birds*, ed. I.A. Orlov, pp. 83–122. Moscow: Nauka. [In Russian]
- Shishkin, M.A., 1980. The Luzocephalidae, a new Triassic labyrinthodont family. *Paleontological Journal* 1980: 88–101.
- Shishkin, M.A., 1992. Russian Triassic amphibians stolen. *Lethaia* 25: 360.
- Shishkin, M.A., & J. Welman, 1994. A new find of *Trematosuchus* (Amphibia, Temnospondyli) from the *Cynognathus* Zone of South Africa. *Palaeontologia africana* 31: 39–49.
- Shishkin, M.A., B.S. Rubidge & J.W. Kitching, 1996. A new lydekkerinid (Amphibia, Temnospondyli) from the Lower Triassic of South Africa—implications for evolution of the early capitosauroid cranial pattern. *Philosophical Transactions of the Royal Society of London B* 351: 1635–1659.
- Steyer, J.S., 2002. The first articulated trematosaur "amphibian" from the Lower Triassic of Madagascar: implications for the phylogeny of the group. *Palaeontology* 45: 771–793.
- Swofford, D.L., 1993. *PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1*. Champaign: Illinois Natural History Survey.
- Warren, A.A., 1980. *Parotosuchus* from the Early Triassic of Queensland and Western Australia. *Alcheringa* 4: 25–36.
- Warren, A.A., & T. Black, 1985. A new rhytidosteid (Amphibia, Labyrinthodontia) from the Early Triassic Arcadia Formation of Queensland, Australia, and the relationships of Triassic temnospondyls. *Journal of Vertebrate Paleontology* 5: 303–327.

- Warren, A.A., R.J. Damiani & A.M. Yates, 2000. Palaeobiogeography of Australian fossil amphibians. *Historical Biology* 15: 171–179.
- Warren, A.A., & M.N. Hutchinson, 1988. A new capitosaurid amphibian from the Early Triassic of Queensland, and the ontogeny of the capitosaur skull. *Palaeontology* 31: 857–876.
- Warren, A.A., & N. Schroeder, 1995. Changes in the capitosaur skull with growth: an extension of the growth series of *Parotosuchus aliciae* (Amphibia, Temnospondyli) with comments on the otic area of capitosaurs. *Alcheringa* 19: 41–46.
- Warren, A.A., & N. Snell, 1991. The postcranial skeleton of Mesozoic temnospondyl amphibians: a review. *Alcheringa* 15: 43–64.
- Watson, D.M.S., 1919. The structure, evolution and origin of the Amphibia. The "Orders" Rhachitomi and Stereospondyli. *Philosophical Transactions of the Royal Society of London B* 209: 1–73.
- Watson, D.M.S., 1962. The evolution of the labyrinthodonts. *Philosophical Transactions of the Royal Society of London B* 245: 219–265.
- Welles, S.P., 1993. A review of the lonchorhynchine trematosaurs (Labyrinthodontia), and a description of a new genus and species from the Lower Moenkopi Formation of Arizona. *PaleoBios* 14: 1–24.
- Welles, S.P., & J.W. Cosgriff, 1965. A revision of the labyrinthodont family Capitosauridae and a description of *Parotosaurus peabodyi* n. sp. from the Moenkopi Formation of Northern Arizona. *University of California Publications in Geological Sciences* 54: 1–148.
- Wiman, C., 1914. Über die Stegocephalen aus der Trias Spitzbergens. Bulletin of the Geological Institution of the University of Uppsala 13: 1–34.
- Yates, A.M., 1999. The Lapillopsidae: a new family of small temnospondyls from the Early Triassic of Australia. *Journal of Vertebrate Paleontology* 19: 302–320.
- Yates, A.M., & A.A. Warren, 2000. The phylogeny of the "higher" temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society* 128: 77–121.

Manuscript received 1 August 2002, revised 20 March 2003 and accepted 3 April 2003.

Associate Editor: G.D. Edgecombe.

# Revision of the Australian Spider Genus *Habronestes* (Araneae: Zodariidae). Species of New South Wales and the Australian Capital Territory

### BARBARA BAEHR

Queensland Museum, PO Box 3300, South Brisbane QLD 4101, Australia BarbaraB@qm.qld.gov.au

ABSTRACT. The genus *Habronestes* L. Koch, 1872 is revised for the species of New South Wales. The genus now contains 28 species Australia-wide, with 23 species recorded from New South Wales. *Habronestes bradleyi* (Pickard-Cambridge, 1869), *Habronestes macedonensis* (Hogg, 1900) and *Habronestes pictus* (L. Koch, 1865), are redescribed and 20 species are newly described as: *H. bicornis* n.sp., *H. driscolli* n.sp., *H. giganteus* n.sp., *H. grahami* n.sp., *H. hebronae* n.sp., *H. helenae* n.sp., *H. hamatus* n.sp., *H. hunti* n.sp., *H. jocquei* n.sp., *H. longiconductor* n.sp., *H. grayi* n.sp., *H. minor* n.sp., *H. monocornis* n.sp., *H. piccolo* n.sp., *H. pseudoaustraliensis* n.sp., *H. ungari* n.sp., *H. raveni* n.sp., *H. raweni* n.sp., *H. weelahensis* n.sp., *H. wilkiei* n.sp. The species are divided between three speciesgroups, according to their eye configuration. A key is provided for the three groups as well as for the species.

BAEHR, BARBARA, 2003. Revision of the Australian spider genus *Habronestes* (Araneae: Zodariidae). Species of New South Wales and the Australian Capital Territory. *Records of the Australian Museum* 55(3): 343–376.

This systematic paper provides the first overview of the large, endemic Australian genus *Habronestes*. As a result of this review, *Habronestes* now contains 28 species, of which only eight were previously described.

This endemic genus is part of the predominantly tropical ant-eating and ant mimicking spider family Zodariidae, one of the most diverse spider families in Australia. They associate with ants and prefer them as food. Studies on *Habronestes bradleyi* (Pickard-Cambridge, 1869) have shown that these spiders not only mimic the body-shape and behaviour but also the pheromones of ants (Allan *et al.*, 1996). Like ants, *Habronestes* species are found mainly in semi-arid areas of Australia.

The genus contains about 80–100 species of small to medium-sized spiders (2.5–10.5 mm). This paper is the first part of the revision of the entire genus and deals only with the fauna of New South Wales and the Australian Capital Territory (ACT).

### Material and methods

All descriptions are generated with the aid of Intkey (Dallwitz *et al.*, 1998) and shortened where possible. Epigynes were cleared in lactic acid. Different drawing methods and kinds of paper were experimented with to get best results for showing characters. Schoellershammer Zeichenpapier, 4G, glatt 250g/m, ref. 010915 and Staedtler omnichrom 108, black pencil and black ink Faber-Castel, seems to be the best combination (e.g., compare Figs. 119, 120—drawn with the aforementioned tools—with 117, 118). Drawings were taken from body, right palp, epigyne and vulva. All measurements are in mm. Detailed spination patterns of legs were not given but special (autapomorphic or synapomorphic) spination characters are mentioned. Colour patterns were described from spiders in alcohol. The white abdominal patches, mentioned in the descriptions,

can be yellow or orange in living spiders. The species are mainly named after the people who collected or recognized the species or in honour of experienced spider experts.

Abbreviations of used morphological terms and institutions from which material was borrowed are as follows:

ALE anterior lateral eyes.

ALE-PLE distance between anterior lateral and posterior lateral eyes

ALS anterior lateral spinnerets

AM Australian Museum (Sydney)

AME-ALE distance between anterior median and anterior lateral eyes

AME anterior median eyes

AME-AME distance between anterior median eyes

cl/cw carapace length/carapace width

DD D. Driscoll (collector)
DTA dorsal tegular apophysis

DTiA dorsal tibial apophysis

G/C Mike Gray and Gerry Cassis (collectors)

LTA lateral tegular apophysis MOQ median ocular quadrangle

NMV Museum Victoria, Melbourne (formerly National Museum of Victoria)

PLE posterior lateral eyes

PLS posterior lateral spinnerets

PME-PLE distance between posterior median and posterior lateral eyes

PME posterior median eyes

PME-PME distance between posterior median eyes

PMS posterior median spinnerets QM Queensland Museum, Brisbane

RCF retrolateral cymbial fold

SA South Australian Museum, Adelaide

SF State Forest

sl/sw sternum length/sternum width

VTA ventral tegular apophysis

VTiA ventral tibial apophysis

ZMH Zoologisches Museum, Hamburg

### **Systematics**

**Type species**. *Habronestes striatipes* L. Koch, 1872 by subsequent designation of Petrunkevitch (1928).

The genus *Habronestes* was first described by L. Koch (1872), but he did not designate a type species. Following R. Jocqué (1991), I agree that *H. striatipes* L. Koch, 1872 must be taken as the type species of *Habronestes*, because it is both the first described species in L. Koch (1872) and first mentioned as a type species by Petrunkevitch (1928). Rainbow (1911) did not designate a type species for *Habronestes* in his catalogue of the Australian Araneida because he listed only it in the synonymy of *Storena*. In contrast to the genus *Storena*, revised by Jocqué & Baehr (1992), all species of *Habronestes* have similar male palpal structure but different abdominal patterns.

The generic description of L. Koch (1872) contains only somatic characters, that are not unique to the genus. Nevertheless, he mentioned the sickle-shaped VTA of the *Habronestes bradleyi* male (1872: 306). According to Jocqué (1991), "the only sure diagnostic character is the Y-shaped tegulum of the male palp [= the sickle-shaped VTA], always combined with a large, lateral, cymbial fold [= the RCF]" (Figs. 1, 3, 5). A third synapomorphic character is the membranous DTA with long stalk and curled end covered with spicules (Figs. 2, 4, 6), that functions as a conductor.

The extremely different eye group patterns (Figs. 7–13) of the examined species suggest that they belong to three different species-groups. I prefer to divide the species into species-groups, rather than in new genera, because the main three synapomorphic characters—the sickle-shaped VTA, the deep retrolateral cymbial fold (RCF) and the membranous stalked DTA of the male palp—occur in all three groups and this suggests that the genus is monophyletic. In addition, all species possess two rows of short ventral spines on tarsi I–IV, a distoventral preening brush on metatarsi II, III and long, strong spines on tibiae and metatarsi III and IV, (hence, these characters are omitted from each species description). Whether all of these characters are synapomorphic for *Habronestes* can be only decided after all Australian zodariid species have been examined.

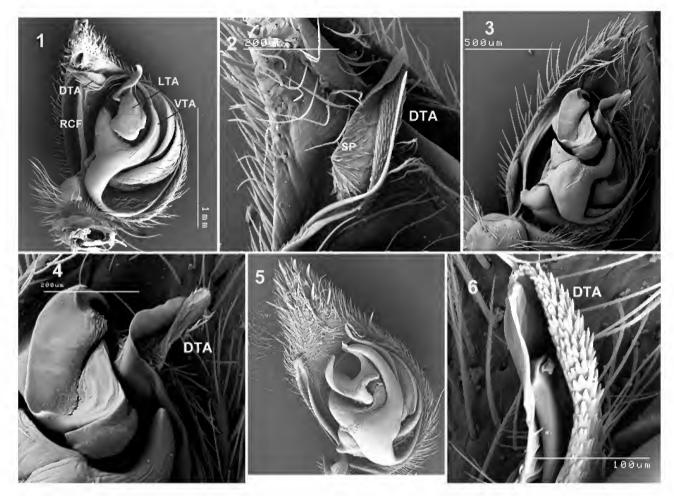
Further studies will show if it is necessary to split the genus as in the *Asteron*-complex (Baehr & Jocqué 1996, 2000, 2001; Jocqué & Baehr, 2001). Species-groups are here named after described species that represent each eye group pattern as: *Habronestes australiensis* species-group, *Habronestes macedonensis* species-group and *Habronestes pictus* species-group (Figs. 7–10). Palps of each group are shown in Figs. 1–6.

#### Genus Habronestes L. Koch

Habronestes L. Koch, 1872: 299; Jocqué, 1991: 56; Jocqué, 1995: 143

**Diagnosis.** Cymbium with large, retrolateral fold (RCF); palp with sickle-shaped VTA; DTA with long stalk and curled end covered with spicules, which functions as a conductor. Tarsi I–IV with 2 rows of short stout ventral spines.

**Description**. Small to medium sized spiders, 2.50–10.50 mm body length. Colour. Carapace, sternum & chelicerae orange or sepia brown; maxillae, labium yellow or pale brown. Abdomen medium or sepia brown with 2-5 pairs of white patches on top and 1-3 single patches in front of spinnerets, laterally pale or sepia brown with 1 or 2 long horizontal white stripes, ventrally pale to sepia brown with or without longitudinal white stripe. Legs yellow or pale brown, clearly annulated or with indistinct colour pattern. Carapace. Oval; raised at front or not raised. Sternum. Heart-shaped, anterior margin straight. Eyes. In 3 rows, 2 4 2, or circular around AME. PLE largest being 2-3× diameter of AME, or AME largest, or all eyes subequal. Clypeus & chilum. Clypeus about 5-6× diameter of ALE. Chilum divided or undivided. *Mouthparts*. Chelicerae, basal segment with rows of hairs, bordering mesial margin, dorsally with a few hairs and bristles; maxillae triangular, with promarginal scopula; labium triangular. Abdomen. Oval; PLS close together; colulus tiny with some hairs; tracheal spiracle small, slit-like with sclerotized cover. Legs. Length formula 4123, 4312 or 4132; tarsi I–IV with 2 rows of short ventral spines; metatarsi II, III with distoventral preening brush; tibiae and metatarsi III, IV with long strong spines; 10–14 teeth on inner side of paired claws; 3rd claw on onychium (Fig. 51). Male palp. Cymbium with RCF occupying from half to whole of cymbium length; with weak dorsal scopula and a few strong spines apically. Tegulum LTA with stalk and irregular plate; DTA chitinous or membranous, with a thin or flattened stalk and a curled

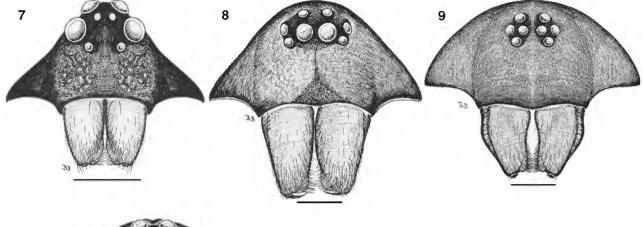


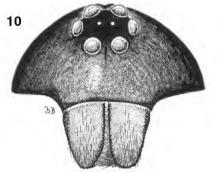
Figs. 1–6. Male palps, ventral view: (1, 2) *Habronestes bradleyi* (Pickard-Cambridge); (3, 4) *Habronestes pseudoaustraliensis* n.sp.; (5, 6) *Habronestes rawlinsonae* n.sp. DTA = dorsal tegular apophysis; DTiA = dorsalateral tibial apophysis; LTA = lateral tegular apophysis; RCF = retrolateral cymbial fold; SP = spicules; VTA = ventral tegular apophysis; VTiA = ventral tibial apophysis.

apical end, covered with spicules; VTA sickle-shaped (Figs. 1–6). Embolus thin and semicircular (only when different mentioned in species description). Tibiae short; with large or small DTiA and short VTiA (Figs. 18–22). *Epigyne*.

Variable, with or without scape, with central or paired opening at posterior margin. Copulatory ducts short or long and coiled ending in ovoid, sometimes contiguous spermathecae.

# Key to Habronestes species-groups of New South Wales



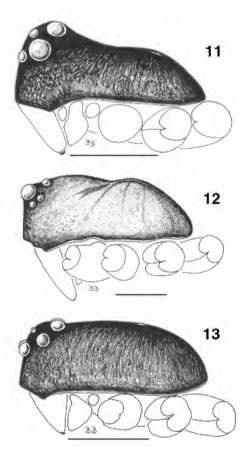


Figs. 7–10. Habronestes faces: (7) Habronestes pseudoaustraliensis n.sp. (Habronestes australiensis species-group); (8) Habronestes rawlinsonae n.sp. (Habronestes macedonensis species-group); (9) Habronestes grayi n.sp.; (10) Habronestes monocornis n.sp. (Habronestes pictus species-group). Scales 0.5 mm.

# Habronestes australiensis species-group

**Diagnosis.** Carapace raised in eye region. Eyes, PLE largest, 2–3× AME. Abdomen medium to sepia brown with 2–4 pairs of white patches on top of abdomen and 2–3 patches in front of spinnerets.

**Description**. Medium-sized spiders, body length 4.00–6.50 mm. Colour. Carapace, sternum, chelicerae orange or sepia brown, iridescent; maxillae, labium, yellow or pale brown. Abdomen medium or sepia brown with 2–4 pairs of white patches on top and 2-3 patches in front of spinnerets; laterally pale or sepia brown with 1 long horizontal white stripe reaching front; ventrally pale to sepia brown. Carapace. Oval, raised at front. Sternum. Heart-shaped, anteriorly straight. Eyes. In 3 rows, 2 4 2. PLE largest 2–3× AME. Eye group width \( \frac{2}{3} - \frac{3}{4} \) of headwidth. Clypeus & chilum. Clypeus about 5-6× diameter of ALE; chilum divided or undivided. Mouthparts. Chelicerae, basal segment with rows of hairs, bordering mesial margin, dorsally with a few hairs and bristles; maxillae triangular, with promarginal scopula; labium triangular. Abdomen. Oval; PLS close together; colulus tiny, with some hairs; tracheal spiracle small, slitlike with sclerotized cover. Legs. Length formula 4312; tarsi I–IV with 2 rows of short ventral spines (Fig. 53); 3rd claw on onychium (Fig. 51). Male palp. Cymbium with RCF occupying from 3/3 to whole of cymbium length; with weak dorsal scopula and a few strong spines apically. Tegulum LTA with short stalk and irregular plate; DTA chitinous or membranous, with a thin or flattened stalk and a curled apical end, covered with spicules (Figs. 3, 4); VTA sickleshaped. Embolus thin and semicircular. Tibiae short; with large or small DTiA and short VTiA (Figs. 18–22).



Figs. 11–13. Habronestes cephalothorax, lateral view: (11) Habronestes pseudoaustraliensis n.sp. (Habronestes australiensis species-group); (12) Habronestes rawlinsonae n.sp. (Habronestes macedonensis species-group); (13) Habronestes monocornis n.sp. (Habronestes pictus species-group). Scales 1 mm.

# Key to new species of the Habronestes australiensis species-group of New South Wales

1	males	2
	- females	4
2	Legs not annulated. Palpal DTiA short. Cymbium strongly bent, RCF reaches tip of cymbium. Embolus originates retrolaterally (Figs. 21, 22)	H. driscolli
	- Legs clearly annulated. Palpal DTiA long. Cymbium not bent, RCF only about $\frac{1}{3}$ of cymbium length. Embolus originates prolaterally (Figs. 17–20)	3
3	Palpal tibia with thick spur on base of DTiA, LTA with 2 sickle-shaped hooks retrolaterally (Figs. 19, 20)	H. hamatus
	- Palpal tibia without thick spur, LTA medially with concavity (Figs. 17, 18)	H. pseudoaustraliensis
4	Epigyne with large, semicircular opening and large, globular spermathecae (Figs. 23, 24)	H. pseudoaustraliensis
	- Epigyne with small, semicircular opening and long, spiralled copulatory ducts (Figs. 25, 26)	H. driscolli

### Habronestes driscolli n.sp.

Figs. 21, 22, 25, 26, 138

Type material. HOLOTYPE  $\eth$ : NSW, Pulletop, 33°58'46"S 146°30'28"E, 24.ii.1999, DD, QM S58544. PARATYPES:  $1 \$  QM S51499,  $1 \$  QM S51540, both same data as holotype.

**Diagnosis.** Carapace yellow orange. Abdomen with 2 pairs of white patches on anterior part and 2–3 patches in front of spinnerets. Cymbium extremely bent, RCF reaching tip. Epigyne with very small central opening.

**Description**. *Male* (holotype). Total length 5.52; carapace 2.32 long, 1.80 wide; 1.16 high; cl/cw 1.29; sternum 1.00 long, 1.00 wide; sl/sw 1.00. Abdomen 3.20 long, 2.40 wide. Colour. Carapace yellow orange, with dark margin; sternum & chelicerae yellow, orange; maxillae & labium yellowish orange, distally white. Abdomen medium brown with 2 pairs of white patches on anterior part and 2-3 patches in front of spinnerets; laterally pale brown with 1 long horizontal white stripe reaching front; ventrally pale brown; legs orange brown to yellow. Carapace. Raised at front. Eyes. In 3 rows, 2 4 2. PLE largest. Eye group width 0.76 of headwidth; AME 0.10; ALE 0.10; PME 0.18; PLE 0.30; AME-AME 0.08; AME-ALE 0.18; ALE-PLE 0.10; PME-PME 0.14; PME-PLE 0.16. MOQ: AME-PME 0.46; AME-AME 0.28; PME-PME 0.50. Clypeus & chilum. Clypeus 0.56 high; chilum divided. Legs. Length formula 4312; femora I-III with 1 row, femur IV with 2 rows of long thin setae ventrally; paired claws with 15 or more teeth. *Male* palp (Figs. 21, 22). RCF deep, running entire length of cymbium, RCF and cymbium strongly bent; cymbium with 4 strong spines apically; DTA with a flattened stalk; VTA with sharp tip; embolus originates retrolaterally. Tibiae short with 2 long prolateral setae, and with a group of bent spines retrolaterally; DTiA as long as ventrolateral apophysis; VTiA short (Fig. 22).

Female (paratype QM S51499). Total length 4.40; carapace 2.20 long, 1.76 wide; 1.12 high; cl/cw 1.25; sternum 0.96 long, 0.96 wide; sl/sw 1.00. Abdomen 2.20 long, 1.48 wide.

Colour. As in male. Eyes. Pattern as in male. Eye group width 0.84 of headwidth; AME 0.10; ALE 0.10; PME 0.18; PLE 0.30; AME-AME 0.08; AME-ALE 0.18; ALE-PLE 0.10; PME-PME 0.14; PME-PLE 0.16. MOQ: AME-PME 0.46; AME-AME 0.28; PME-PME 0.50. Clypeus 0.56 high. Epigyne (Figs. 25, 26). With small posterior oval to semicircular opening. Vulva with extremely long, spiralled copulatory ducts ending in almost touching spermathecae.

**Distribution**. Known only from type locality in western New South Wales (Fig. 138).

**Etymology**. Species name is a patronym in honour Dr Don Driscoll, the collector of the type.

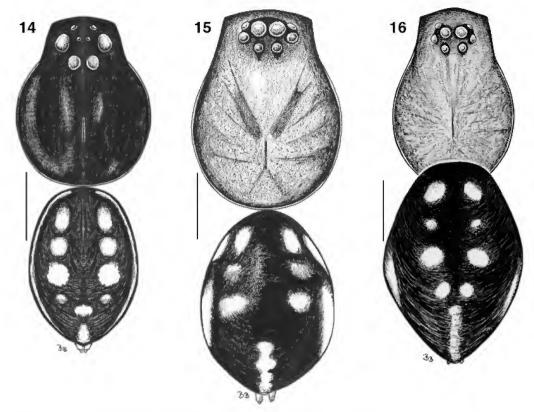
### Habronestes hamatus n.sp.

Figs. 19, 20, 138

**Type material**. HOLOTYPE &: NSW, Pulletop, 33°58'46"S 146°30'28"E, 24.ii.1999, D. Driscoll, QM S51505.

**Diagnosis**. Carapace sepia brown. Abdomen with 4 pairs of white patches on top and 2 patches in front of spinnerets. Male palp with VTA hidden by extremely large LTA; tibia with a thick spine retrolaterally at base of large, dorsolateral tibial apophysis.

**Description**. *Male* (holotype). Total length 5.52; carapace 2.80 long, 2.00 wide; 1.28 high; cl/cw 1.40; sternum 1.40 long, 1.16 wide; sl/sw 1.21. Abdomen 2.72 long, 1.76 wide. *Colour*. Carapace sepia brown, iridescent; sternum reddish brown; chelicerae medium brown; maxillae, labium pale brown, bases darker brown. Abdomen sepia brown with 4 pairs of white patches on top and 2 patches in front of spinnerets; laterally sepia brown with 1 long horizontal white stripe reaching front; ventrally pink brown; legs medium brown with indistinct colour pattern; legs I–IV with pale brown coxa and sepia brown femur. *Carapace*. Raised at front. *Sternum*. Heart-shaped anteriorly straight; with lateral margin produced between coxae and intercoxae; glossy. *Eyes*. In 3 rows 2 4 2. PLE largest. Eye group width



Figs. 14–16. Habronestes body, dorsal view: (14) Habronestes pseudoaustraliensis n.sp.; (15) Habronestes rawlinsonae n.sp.; (16) Habronestes hebronae n.sp. Scales 1 mm.

0.7 of head width; AME 0.12; ALE 0.12; PME 0.18; PLE 0.30; AME-AME 0.06; AME-ALE 0.10; ALE-PLE 0.08; PME-PME 0.14; PME-PLE 0.14. MOQ: AME-PME 0.50; AME-AME 0.30; PME-PME 0.50. Clypeus & chilum. Clypeus 0.72 high; chilum undivided, long. Male palp (Figs. 19, 20). RCF ½ of the cymbium length. LTA with t-shaped horizontal plate and 2 large hooks retrolaterally; DTA with thin stalk; VTA with blunt tip. Tibiae short; DTiA 1.5 as long as tibia, with thick basal spine.

Female. Unknown.

**Distribution**. Known only from type locality in western New South Wales (Fig. 138).

**Etymology**. Species name is an adjective (Latin: *hamatus* = with hooks) taken because of the large hooks on the retrolateral part of the LTA of the male palp.

### Habronestes pseudoaustraliensis n.sp.

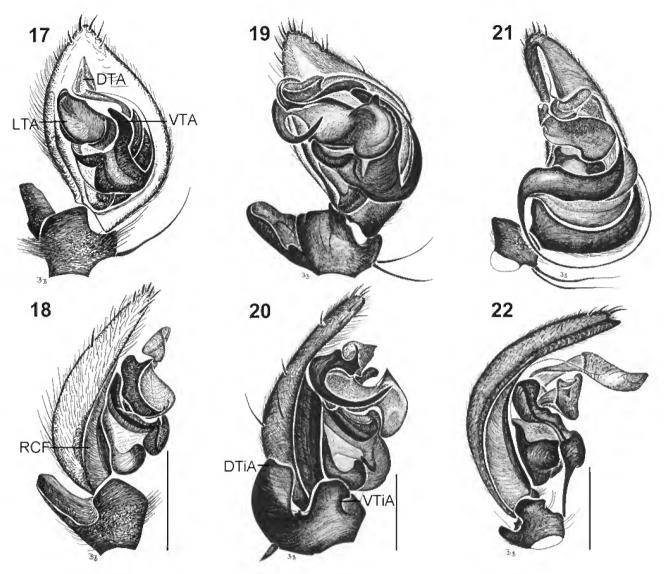
Figs. 3, 4, 17, 18, 23, 24, 53, 138

**Type material**. HOLOTYPE &: NSW, Weelah SF, 33°21'51"S 147°15'2"E, 25.iii.1996, Callitris forest F4 Trap C1, 21–28 Mar 1996, D. Smith & R. Harris, AM KS49573. PARATYPES: 1& same data as holotype but coll. Trap A3, AM KS55704; 1& 10 km N of Girral on Girral-Condobolin Rd, 33°39'43"S 147°4'6"E, 28.iii.1996, roadside corridor vegetation, 21–28 Mar 1996, D. Smith & R. Harris, AM KS50849; 2& & 35 km S of Burcher on Burcher-W Wyalong Rd, 33°45'12"S 147°18'56"E, 28.iii.1996, roadside corridor vegetation, 21–28 Mar 1986, D. Smith & R. Harris, AM KS50879; 1& Gubatta, 33°32'0"S 146°31'28"E, 24–28.ii.1999, DD, QM S52128; 2& & as previous, QM S50833; 1& Gubatta, 33°38'10"S 146°33'8"E, 24.ii.1999, DD, QM S50875; 2& & Gubatta,

33°34'33"S 146°34'36"E, 24–28.ii.1999, DD, QM S50935; 1& Gubatta, 33°38'7"S 146°33'12"E, 24–28.ii.1999, DD, QM S50955; 1& Gubatta, 33°34'50"S 146°35'36"E, 24.ii.1999, DD, QM S51551; 1& Taleeban Woodland, 33°56'29"S 146°25'8"E, 23–27.ii.1999, DD, QM S51004; 1& as previous but coll. 18.x.1999, QM S39689; 1& Taleeban Woodland, 33°57'42"S 146°26'52"E, 23–27.ii.1999, DD, QM S50866; 1& Taleeban Woodland, 33°57'36"S 146°24'66"E, 18.x.1999, DD, QM S53090; 2&9 as previous QM S53230; 1&0 Ungarie SF, 33°39'44"S 147°4'6"E, 25.iii.1996, Callitris forest F2 trap C2, 21–28 Mar 1996, D. Smith & R. Harris, AM KS49590.

**Diagnosis.** With 4 pairs of white patches on top of abdomen and 2 patches in front of spinnerets; tibia with long LTiA. Epigyne with semicircular opening. Vulva with large, contiguous globular spermathecae.

**Description**. *Male* (holotype). Total length 4.40; carapace 2.24 long, 1.72 wide; 0.96 high; cl/cw 1.30; sternum 1.12 long, 1.00 wide; sl/sw 1.12. Abdomen 2.16 long, 1.40 wide. *Colour*. Carapace, sternum, chelicerae sepia brown, iridescent. Maxillae pale brown; labium sepia brown. Abdomen (Fig. 14) sepia brown with 4 pairs of white patches on top and 2 patches in front of spinnerets; ventrally and laterally sepia brown with 1 long horizontal white stripe reaching front. Legs medium brown with indistinct colour pattern; legs I-IV with pale brown coxa, sepia brown femur. Carapace. Raised at front. Eyes. In 3 rows 2 4 2. PLE largest. Eye group width 0.75 of head width; AME 0.08; ALE 0.12; PME 0.18; PLE 0.26; AME-AME 0.06; AME-ALE 0.16; ALE-PLE 0.06; PME-PME 0.10; PME-PLE 0.16. MOQ: AME-PME 0.44; AME-AME 0.22; PME–PME 0.46. Clypeus & chilum. Clypeus 0.56 high; chilum divided. Male palp (Figs. 17, 18). RCF 3/3 cymbium length. LTA half moon-shaped with median concavity; DTA with thin stalk; VTA with blunt tip; embolus originating



Figs. 17–22. *Habronestes australiensis* species-group male palps, ventral view (above), lateral view (below): (17–18) *Habronestes pseudoaustraliensis* n.sp.; (19–20) *Habronestes hamatus* n.sp.; (21–22) *Habronestes driscolli* n.sp. Scale 0.5 mm. DTA = dorsal tegular apophysis; DTiA = dorsolateral tibial apophysis; LTA = lateral tegular apophysis; RCF = retrolateral cymbial fold; VTA = ventral tegular apophysis; VTiA = ventral tibial apophysis.

prolaterally. Tibia short, with 1 long prolateral seta, and with a group of bent spines retrolaterally; DTiA 1.5× as long as tibia; VTiA short.

Female (paratype QM S53230). Total length 6.40; carapace 2.96 long, 2.00 wide; 1.40 high; cl/cw 1.48; sternum 1.36 long, 1.20 wide; sl/sw 1.13. Abdomen 3.44 long, 2.48 wide. *Colour*. Same as male. *Eyes*. Pattern as in male. Eye group width 0.64 of headwidth; AME 0.12; ALE 0.14; PME 0.24; PLE 0.3; AME–AME 0.04; AME–ALE 0.18; ALE–PLE 0.1; PME–PME 0.14; PME–PLE 0.12. MOQ. AME–PME 0.54; AME–AME 0.28; PME–PME 0.62. Clypeus 0.68 high. *Legs*. Same as male. *Epigyne* (Figs. 23, 24). With semicircular opening. Vulva with extremely short copulatory ducts ending in large globular, contiguous spermathecae.

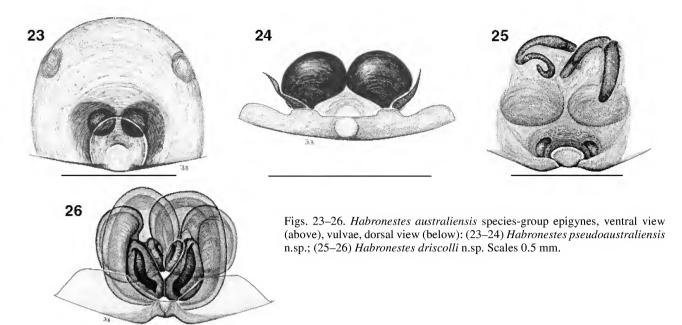
**Distribution**. Western New South Wales (Fig. 138).

**Etymology**. Refers to the similarity to the type species of the species-group *H. australiensis*.

### Habronestes macedonensis species-group

**Diagnosis.** Carapace not raised in front; highest point just behind eye region. Eyes in 2 rows, both rows procurved, AME largest. Femora III, IV with a row of 3–6 stout dorsal spines at distal end; patella III, IV with 1 irregular longitudinal row of stout spines prolaterally. Abdomen with 2–4 pairs of white patches on anterior part and 1 or 2 patches in front of spinnerets.

**Description.** Medium-sized spiders, 4.60–9.70 mm body length. *Colour*. Carapace chestnut brown with dark fovea and dark bifurcate or radiate stripes in front; sternum yellow, reddish or pale brown; chelicerae medium or reddish brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 2–4 pairs of white patches on anterior part, and 1 or 2 long and undulate patches in front of spinnerets; laterally sepia brown or pink brown with 2–3 elongate and broad white patches; ventrally pale pink brown usually with longitudinal white stripe. Legs yellow or pale

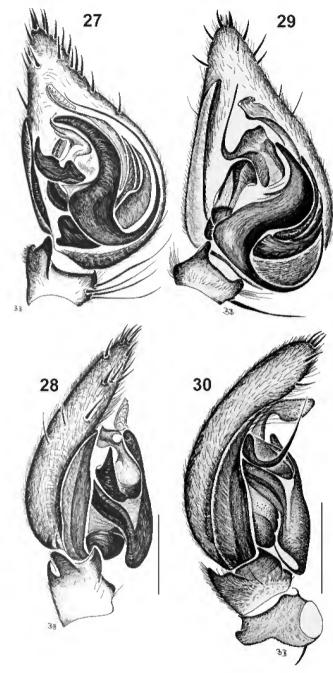


brown; clearly annulated or indistinct colour pattern *Carapace*. Oval, highest just behind eyes. *Sternum*. Heartshaped, anteriorly straight, finely reticulated. *Eyes*. In 2 rows, each with 4 eyes, both rows procurved. AME largest. Eye group width 0.54–0.6 of headwidth. *Clypeus & chilum*. Clypeus about 3× diameter of AME; chilum undivided. *Mouthparts*. Chelicerae, basal segment with rows of hairs, bordering mesial margin, dorsally hirsute, laterally with condyle; maxillae triangular, with promarginal scopula;

labium triangular. *Legs*. Length formula 4132; femora III, IV with a row of 3–6 stout dorsal spines at distal end; patella III, IV with 1 irregular longitudinal row of stout spines prolaterally; 3rd claw on onychium, (Fig. 51). *Male palp*. RCF ½–¾ of cymbium length; LTA with an irregular plate; DTA chitinous, with a flattened or thin stalk and an curled apical end covered with spicules; VTA sickle-shaped, long, with rounded or sharp tip; embolus thin, or semicircular. Tibiae with short apophyses.

# Key to species of the Habronestes macedonensis species-group of New South Wales

1	Males Females	
2	Palpal patella with dorsal apophysis, LTA with long retrolateral spine (Figs. 29, 30, 48)	H. hebronae
	- Palpal patella without dorsal apophysis, LTA without long retrolateral spine (Figs. 46, 47, 49, 50)	3
3	Metatarsus I without special spination ventrally	4
	- Metatarsus I with band of conical thorn-like spines ventrally	
4	Sickle-shaped VTA extremely long, reaching over tegulum (Figs. 27, 28, 50)	H. rawlinsonae
	- Sickle-shaped VTA short and blunt, LTA half moon-shaped with dorsal spine (Figs. 44, 45, 49)	H. ungari
6	LTA fan-shaped with serrated margin retrolaterally (Figs. 40, 41, 46)	H. macedonensis
	- LTA not fan-shaped (Figs. 42, 43, 47)	H. weelahensis
7	Epigyne with w-shaped scape, spermathecae globular, not touching (Figs. 35, 36)	H. macedonensis
	- Epigyne with paired oval openings (Figs. 31–34)	8
8	Epigyne with long oval openings, and s-shaped copulatory ducts (Figs. 31, 32)	H. rawlinsonae
	- Epigyne with broad oval openings, and sausage-like copulatory ducts (Figs. 33, 34)	H. hebronae



Figs. 27–30. *Habronestes macedonensis* species-group male palps, ventral view (above), lateral view (below): (27–28) *Habronestes rawlinsonae* n.sp.; (29–30) *H. hebronae* n.sp. Scales 0.5 mm.

## Habronestes macedonensis (Hogg, 1900)

Figs. 35, 36, 37, 40, 41, 46, 139

Storena macedonensis Hogg, 1900: 2, 97, 98, pl. 14, fig. 4 (description male); Rainbow, 1911:150 (description male). Habronestes macedonensis.—Jocqué, 1995: 145, fig. 3c,d (description male).

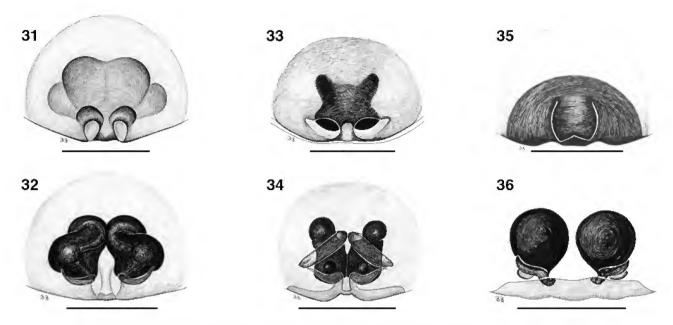
**Remarks**. The male of *Habronestes macedonensis* was first described by Hogg, 1900 as *Storena macedonensis*. Jocqué (1995) has reexamined the holotype and placed the species in *Habronestes* because of the special palp structure. The female is described here for the first time.

Material examined. 1♀, 1♂: NSW, Washpool NP Grassy Ck, where crossed by North West Fire Trail/Washpool Trail, 29°27'43"S 152°16'22"E, 4.ii–9.iv.1993, 900 m, G/C, AM KS36298; 1♀, 1♂ as previous, QM S60828; 1♂ Conglomerate SF, 100 m SW of jnctn of Hallgraths Trail & Sherwood Rd, 30°7'0"S 153°3'14"E, 4.ii–9.iv.1993, 320 m, G/C, AM KS39028; 1♂ Hazelbrook, 33°44'S 150°27'E, 4.ii.1979, M. Dingley, AM KS3037; 1♂ Warra SF, 2.8 km W of Moggs Swamp Ck, Moggs Swamp Fire Trail, 29°59'19"S 151°57'14"E, 4.ii–9.iv.1993, 1140 m, G/C, AM KS36361; 1♂ Warra SF, Moggs Swamp Fire Trail, 2.5 km N of Moggs Swamp Ck, 29°57'32"S 151°58'18"E, 4.ii–9.iv.1993, 1170 m, G/C, AM KS36370; 1♂ Rocky Waterholes Rd, Beaury SF, 28°32'49"S 152°20'11"E, 9.iv.1993, 4.ii–9.iv.1993, 705 m, G/C, AM KS56172. ACT: 1♂ Tidbinbilla SF, 35°26'S 148°56'E, litter, P. Ormay, AM KS3535.

**Diagnosis**. Eyes in 2 rows, both rows procurved, AME largest. Abdomen with 2 pairs of white patches on anterior part, the first elongated and nearly divided in two; and 2 patches in front of spinnerets. Metatarsus I with irregular band of short strong spines ventrally in males. LTA fanshaped covered with small spicules (Figs. 40, 41). Epigyne with w-shaped scape. Vulva with extremely short copulatory ducts ending in large, globular, not touching spermathecae (Figs. 35, 36).

**Description**. *Male* (AM KS36298). Total length 6.24; carapace 3.44 long, 2.24 wide; 1.32 high; cl/cw 1.53; sternum 1.40 long, 1.36 wide; sl/sw 1.02. Abdomen 2.8 long, 2.16 wide. *Colour*. Carapace chestnut brown with dark fovea and dark bifurcate patches in front; sternum yellow brown; chelicerae medium brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 2 pairs of white patches on anterior part, the first elongated and nearly divided in two and 1 long and undulate patch in front of spinnerets; laterally sepia brown with 2–3 long and broad white patches; ventrally pale pink brown. Legs yellow; clearly annulated; legs I-IV with white coxa, prolateral suture sepia brown, pale trochanter, proximal ½ of femora white and distal ½ sepia brown with darker brown lateral stripes on patella and tibiae III, IV. Eyes. In 2 rows each with 4 eyes, both rows procurved. AME largest. Eye group width 0.6 of head width; AME 0.24; ALE 0.16; PME 0.16; PLE 0.16; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.04; PME-PME 0.16; PME-PLE 0.16. MOQ. AME-PME 0.52; AME-AME 0.52; PME-PME 0.48. Clypeus & chilum. Clypeus 0.60 high; chilum undivided, short. Legs. Length formula 4132; metatarsus I with irregular band of short, strong spines ventrally; femora III, IV with a row of 5-6 stout dorsal spines at distal end; patella III, IV with 1 irregular longitudinal row of stout spines prolaterally. Male palp (Figs. 40, 41, 46). Cymbium with flat RCF, ½ of the cymbium length. LTA with a thick, turned vertical stalk and with a sickle-shaped plate serrated on retrolateral margin; DTA chitinous, with a flattened stalk and a curled apical end covered with spicules; VTA sickle-shaped, long, with rounded tip. Tibiae short; with 1 long prolateral seta and with a group of bent spines retrolaterally; DTiA with chitinous rim, triangular; VTiA short and triangular.

Female (AM KS36298). Total length 8.72; carapace 4.32 long, 3.00 wide; 2.00 high; cl/cw 1.50; sternum 1.64 long, 1.60 wide; sl/sw 1.02. Abdomen 4.40 long, 3.20 wide. Colour. Same as male. Eyes. In 2 rows each with 4 eyes, both rows procurved. AME largest. Eye group width 0.54 of head width; AME 0.30; ALE 0.2; PME 0.20; PLE 0.20; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.04; PME-PME 0.20; PME-PLE 0.20. MOQ: AME-PME 0.68; AME-PME A



Figs. 31–36. *Habronestes macedonensis* species-group epigynes, ventral view (above), vulvae, dorsal view (below): (31–32) *Habronestes rawlinsonae* n.sp.; (33–34) *Habronestes hebronae* n.sp.; (35–36) *Habronestes macedonensis* (Hogg). Scales 0.5 mm.

AME 0.64; PME–PME 0.60. Clypeus 1.12 high. *Epigyne* (Figs. 35, 36). With w-shaped scape. Vulva with extremely short copulatory ducts ending in large globular, not touching spermathecae.

**Distribution**. Victoria, northeastern New South Wales and ACT (Fig. 139).

#### Habronestes hebronae n.sp.

Figs. 16, 29, 30, 33, 34, 48, 139

**Type material.** Holotype ♂: NSW, Pulletop, 34°0′6″S 146°5′10″E, 24–28.ii.1999, DD, QM S50998. Paratypes: same data as holotype: 1 ♂ QM S50998, 2 ♂ QM S51516, 1 ♂ QM S50997; 1 ♂ Gubatta, 33°34′33″S 146°34′36″E, 28.ii.1999, DD, QM S51002; 1 ♂ Pulletop, 33°58′10″S 146°4′50″E, 24–28.ii.1999, DD, QM S39856; 3 ♂ ♂ Pulletop, 33°58′46″S 146°3′28″E, 24–28.ii.1999, DD, QM S51501; 4 ♂ ♂ Pulletop, 33°58′55″S 146°4′46″E, 24–28.ii.1999, DD, QM S51602; 1 ♂ Taleeban Woodland, 33°55′53″S 146°28′23″E, 23–27.ii.1999, DD, QM S50831; 1 ♀ Taleeban Woodland, 33°57′55″S 146°26′39″E, 27.ii.1999, DD, QM S50920.

**Diagnosis.** With 4 pairs of white patches on top of abdomen and 1 long patch in front of spinnerets. Tibia I with a band of conical, thorn-like spines ventrally in males. LTA with retrolateral thorn. Palpal patella with dorsolateral apophysis (Figs. 29, 30). Epigyne with paired broad-oval openings. Vulva with sausage-shaped copulatory ducts ending at posteriorly touching spermathecae (Figs. 33, 34).

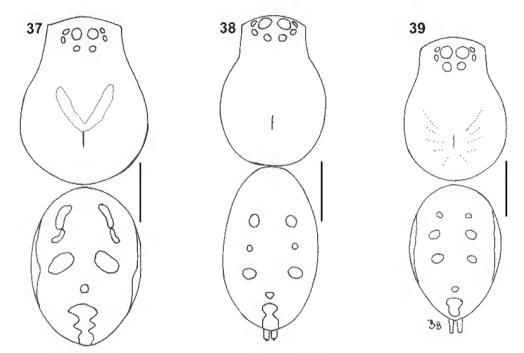
**Description**. *Male* (holotype). Total length 4.64; carapace 2.32 long, 1.80 wide; 1.16 high; cl/cw 1.28; sternum 1.04 long, 1.00 wide; sl/sw 1.04. Abdomen 2.32 long, 1.52 wide. *Colour*. Carapace chestnut brown with dark fovea and dark radiating stripes; sternum and chelicerae reddish brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 4 pairs of white patches on top and 1 long patch in front of spinnerets; laterally sepia brown with 2 long, white patches equal in length; ventrally pink brown with 1 longitudinal white stripe from epigastric fold to near tracheal spiracle. Legs pale brown with indistinct colour pattern;

legs I, II, III, IV with coxa and trochanter white, proximal ½ of femora white and distal ½ sepia brown; leg II with darker brown lateral stripes on patella and tibia. Sternum. With lateral margin produced between coxae; finely reticulated. Eyes. In 2 rows each with 4 eyes, both rows procurved. AME largest. Eye group width 0.58 of headwidth; AME 0.18; ALE 0.12; PME 0.12; PLE 0.12; AME-AME 0.04; AME-ALE 0.02; ALE-PLE 0.02; PME-PME 0.10; PME-PLE 0.10. MOQ: AME-PME 0.40; AME-AME 0.40; PME-PME 0.34. Clypeus & chilum. Clypeus 0.56 high; chilum undivided short. Legs. Length formula 4312; tibia I with a band of conical, thorn-like spines ventrally; femora III, IV with a row of 3-4 stout dorsal spines at distal end; patella III, IV with 1 irregular longitudinal row of stout spines prolaterally. Male palp (Figs. 29, 30, 48). RCF deep, 3/3 of the cymbium length. LTA with sickle-shaped plate (Fig. 48); DTA with a thin stalk; VTA with acute tip. Tibiae short; with 2 long prolateral setae; DTiA short rounded; patella with dorsolateral apophysis.

Female (paratype, QM S50920). Total length 5.76; carapace 2.68 long, 1.92 wide; 1.16 high; cl/cw 1.39; sternum 1.20 long, 1.20 wide; sl/sw 1.00. Abdomen 3.08 long, 2.12 wide. Colour. Same as male. Eyes. AME largest. Eye group width 0.6 of headwidth; AME 0.20; ALE 0.14; PME 0.14; PLE 0.14; AME—AME 0.06; AME—ALE 0.04; ALE—PLE 0.04; PME—PME 0.12; PME—PLE 0.12. MOQ: AME—PME 0.48; AME—AME 0.46; PME—PME 0.40. Clypeus & chilum. Clypeus 0.68 high; chilum undivided short. Legs. Femora III, IV with a row of 3—4 stout dorsal spines at distal end; patella III, IV with 1 irregular, longitudinal row of stout spines prolaterally. Epigyne (Figs. 33, 34). With paired broad-oval openings. Vulva with sausage-shaped copulatory ducts ending at posteriorly touching spermathecae.

Distribution. Western New South Wales (Fig. 139).

**Etymology**. Species name is a patronym in honour of Mrs Wendy Hebron of the Queensland Museum, who recognized the species as new.



Figs. 37–39. Habronestes macedonensis species-group body, dorsal view. (37) Habronestes macedonensis (Hogg); (38) Habronestes ungari n.sp.; (39) Habronestes weelahensis n.sp. Scales 1 mm.

# Habronestes rawlinsonae n.sp.

Figs. 15, 27, 28, 31, 32, 50, 139

**Type material**. Holotype ♂: NSW, Gubatta, 33°32'0"S 146°31'28"E, 24–28.ii.1999, DD, QM S51007. PARATYPES: same data as holotype: 6 \$\displaystyle \displaystyle \disp QM S51003, 2&& QM S50824; 1& Gubatta, 33°38'7"S 146°33'12"E, 24-28.ii.1999, DD, QM S50907; 7&& as previous, QM S50954; 1& Gubatta, 33°34'33"S 146°34'36"E, 24–28.ii.1999, DD, QM S50936; 18 as previous QM S51015; 13 Gubatta, 33°34'50"S 146°35'36"E, 24-28.ii.1999, DD, QM S51535; 1 d Pulletop, 33°57'57"S 146°4'46"E, 24-28.ii.1999, DD, QM S50938; 23 3 as previous, QM S51582; 13 Pulletop, 33°58'10"S 146°4'50"E, 24–28.ii.1999, DD, QM S50978; 3♂♂ as previous, QM S51545; 20 of Pulletop, 34°0'6"S 146°5'10"E, 24-28.ii.1999, DD, QM S50996; 1 & as previous, QM S51515; 3 & & Pulletop, 33°58'46"S 146°3'28"E, 24–28.ii.1999, DD, QM S51502; 1& Pulletop, 34°0′59"S 146°4′15"E, 24–28.ii.1999, DD, QM S51519; 1♂ as previous, QM S51520; 2& & as previous, QM S51572; 1& Pulletop, 33°58'55"S 146°4'46"E, 24.ii.1999, DD, QM S51589; 2 d d as previous, QM S51601; 1d Taleeban Woodland, 33°57'55"S 146°26'39"E, 23-27.ii.1999, DD. OM S50854; 2♂♂ Taleeban Woodland, 33°56'29"S 146°25'8"E, 23–27.ii.1999, DD, QM S50899.

**Diagnosis.** Abdomen with 3 pairs of white patches dorsally and 1 patch in front of spinnerets. VTA extremely long. Epigyne with 2 long, oval openings.

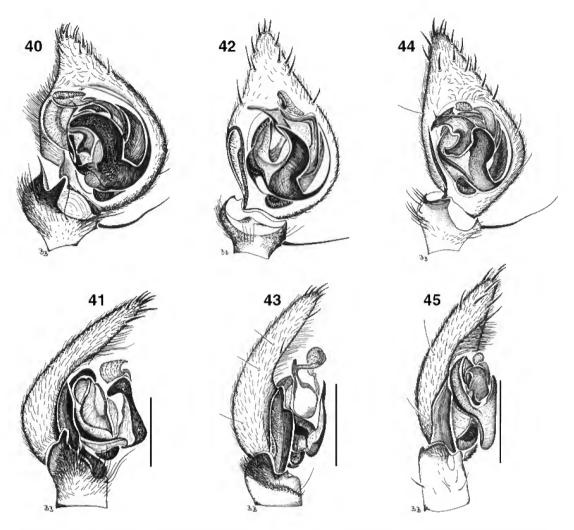
**Description**. *Male* (holotype). Total length 6.52, carapace 3.4 long, 2.56 wide; 1.20 high; cl/cw 1.32; sternum 1.52 long, 1.44 wide; sl/sw 1.05. Abdomen 3.12 long, 2.24 wide. *Colour*. Carapace chestnut brown, iridescent; with dark fovea and dark bifurcate patches in front; sternum yellow brown; chelicerae reddish brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 2–3 pairs of white patches on anterior part and 1 long and undulate patch in front of spinnerets; laterally sepia brown with 2 long and broad white patches; ventrally pink brown. Legs yellow; clearly annulated; legs I–IV with white coxa, prolateral suture sepia brown, pale trochanter, proximal

margin of femora sepia brown, proximal ½ white and distal ½ sepia brown with darker brown lateral stripes on patella and tibia. Eyes. In 2 rows each with 4 eyes, both rows procurved. AME largest. Eye group width 0.58 of headwidth; AME 0.28; ALE 0.20; PME 0.20; PLE 0.20; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.02; PME-PME 0.14; PME-PLE 0.14. MOQ: AME-PME 0.54; AME-AME 0.60; PME-PME 0.54. Clypeus & chilum. Clypeus 0.64 high; chilum undivided short. Legs. Length formula 4123; femora III, IV with a row of 5–6 stout, dorsal spines at distal end; patella III, IV with 1 irregular, longitudinal row of stout spines prolaterally. *Male palp* (Figs. 5, 6, 27, 28, 50). RCF deep, ½ of the cymbium length; LTA with sickle-shaped plate with spines; DTA with a thin stalk; VTA with blunt tip, extremely long, reaching margin of bulb. Tibiae short; with 2 long prolateral setae; DTiA short rounded; VTiA (Fig. 28).

Female (paratype QM S51596). Total length 9.66; carapace 4.58 long, 3.16 wide; 2.04 high; cl/cw 1.45; sternum 1.80 long, 1.80 wide; sl/sw 10. Abdomen 5.08 long, 3.58 wide. Colour. Same as male. Eyes. Pattern as in male. Eye group width 0.55 of headwidth; AME 0.32; ALE 0.20; PME 0.20; PLE 0.20; AME-AME 0.06; AME-ALE 0.04; ALE-PLE 0.06; PME-PME 0.22; PME-PLE 0.24. MOQ. AME-PME 0.72; AME-AME 0.70; PME-PME 0.62. Clypeus & chilum. Clypeus 0.84 high; chilum undivided, short. Epigyne (Figs. 31, 32). With small, paired, long-oval openings. Vulva with kidney-shaped, anteriorly touching copulatory ducts ending in globular spermathecae.

**Distribution**. Western New South Wales (Fig. 139).

**Etymology**. Species name is a patronym in honour of Mrs Wendy Hebron, formerly Rawlinson, of the Queensland Museum, who recognized the species as new.



Figs. 40–45. *Habronestes macedonensis* species-group male palps, ventral view (above), lateral view (below): (40–41) *Habronestes macedonensis* (Hogg); (42–43) *Habronestes weelahensis* n.sp.; (44–45) *Habronestes ungari* n.sp. Scales 0.5 mm.

# Habronestes ungari n.sp.

Figs. 38, 44, 45, 49, 139

**Type material**. HOLOTYPE &: NSW, Ungarie SF, 33°39'44"S 147°4'6"E, 25.iii.1996, *Callitris* forest F2 Trap B4, 21–28 Mar 1996, D. Smith & R. Harris, AM KS83934. PARATYPE: 1 & same data as holotype, AM KS49586.

**Diagnosis.** Abdomen with 3 pairs of white patches dorsally, and 2 patches in front of spinnerets. Male palp, with LTA with a short vertical stalk and sickle-shaped plate with dorsal spines. VTA sickle-shaped, extremely short, with rounded tip. Palpal tibia without real tibial apophysis.

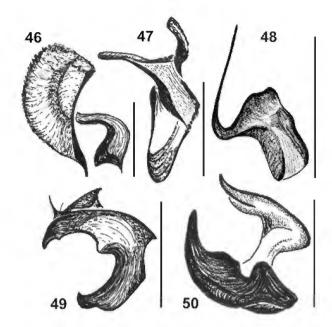
**Description**. *Male* (holotype). Total length 6.16; carapace 3.00 long, 2.00 wide; 1.20 high; cl/cw 1.50; sternum 1.44 long, 1.20 wide. Abdomen 3.16 long, 1.76 wide. *Colour*. Carapace chestnut brown with dark fovea and dark radiating stripes; sternum pale brown; chelicerae medium brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 3 pairs of white patches on anterior part and 2 patches in front of spinnerets; laterally with 2 long white patches, first one larger; ventrally medium brown.

Legs pale brown with indistinct colour pattern; legs I–IV with coxa and trochanter white, proximal 1/2 of femora white and distal ½ sepia brown, darker brown lateral stripes on patella and tibia. Eyes. In 2 rows each with 4 eyes, both rows procurved. AME largest. AME 0.27; ALE 0.18; PME 0.18; PLE 0.18; AME-AME 0.02; AME-ALE 0.04; ALE-PLE 0.04; PME-PME 0.12; PME-PLE 0.14, MOO, AME-PME 0.58; AME-AME 0.56; PME-PME 0.48. Clypeus & chilum. Clypeus 0.48 high; chilum undivided, short. Legs. Length formula 4123; femora III, IV with a row of 3-4 stout dorsal spines at distal end; patella III, IV with 2 longitudinal rows of stout spines prolaterally. Male palp (Figs. 44, 45, 49). RCF flat, ½ of the cymbium length; LTA with sickleshaped plate and dorsal spines. DTA with a thin stalk; VTA sickle-shaped, extremely short with rounded tip; tibiae without real tibial apophysis, with 1 long prolateral seta.

Female. Unknown.

**Distribution**. Known only from type locality in western New South Wales (Fig. 139).

**Etymology**. Species name is taken from the type locality.



Figs. 46–50. Habronestes macedonensis species-group male palps, LTA, ventral view: (46) Habronestes macedonensis (Hogg); (47) Habronestes weelahensis n.sp.; (48) Habronestes hebronae n.sp.; (49) Habronestes ungari n.sp.; (50) Habronestes rawlinsonae n.sp. Scales 0.25 mm.

#### Habronestes weelahensis n.sp.

Figs. 39, 42, 43, 47, 139

**Type material.** Holotype ♂: NSW, Weelah SF, 33°21'51"S 147°15'2"E, 25.iii.1996, *Callitris* forest F4 trap C1, 21–28 Mar 1996, D. Smith & R. Harris, AM KS56090. PARATypes: 1♂20 km N of Burcher on rd to Manna Mtn, 33°22'12"S 147°15'2"E, 25.iii.1996, roadside corridor vegetation N5 Trap A2, 21–28 Mar 1996, D. Smith & R. Harris, AM KS49559; 2♂♂Boundary Ck SF, 0.45 km SW along Boundary Ck Rd from jnctn of Dungel & Shannon Ck Rds, 29°56'48"S 152°33'27"E, 4.ii–9.iv.1993, 600 m, G/C, AM KS39411; 1♂as previous, QM S60630; 1♂

second gully N of Wonga Gully, 30°48'39"S 152°7'26"E, 4.ii–9.iv.1993, 270 m, G/C, AM KS39412.

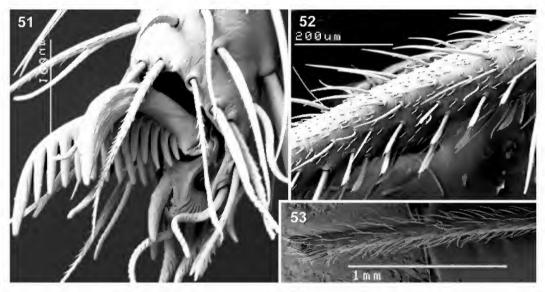
**Diagnosis.** Abdomen with 3 pairs of white patches dorsally, and 2 patches in front of spinnerets. Metatarsus I with 1 row of about 15 small spines ventrally in males.

**Description**. *Male* (holotype). Total length 4.96; carapace 2.52 long, 1.76 wide; 1.16 high; cl/cw 1.43; sternum 1.20 long, 1.08 wide. Abdomen 2.44 long, 1.68 wide. Colour. Carapace chestnut brown with dark fovea and dark radiate stripes; sternum pale brown; chelicerae medium brown; maxillae, labium pale brown, distally white. Abdomen pink brown with 3 pairs of white patches on anterior part and 2 patches in front of spinnerets; laterally pink brown with 2 long white patches, first one broad; ventrally pink brown. Legs vellow brown with indistinct colour pattern; legs I-IV with coxa and trochanter white, proximal ½ of femora white and distal ½ sepia brown, darker brown lateral stripes on patella and tibia. Eyes. Pattern as in male. AME 0.20; ALE 0.14; PME 0.14; PLE 0.14; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.04; PME-PME 0.12; PME-PLE 0.12. MOQ: AME-PME 0.40; AME-AME 0.44; PME-PME 0.40. Clypeus & chilum. Clypeus 0.44 high; chilum undivided, long. Legs. Length formula 4123; metatarsus I with irregular band of short spines ventrally; femora III, IV with a row of 5-6 stout, dorsal spines at distal end; patella III, IV with 1 irregular, longitudinal row of stout spines prolaterally. Male palp (Figs. 42, 43, 47). RCF deep, ½ of the cymbium length; LTA with 2 long horns apically; DTA with a flattened stalk; VTA long with blunt tip. Tibiae short; with 1 long prolateral seta, and with group of bent spines retrolaterally; DTiA short rounded.

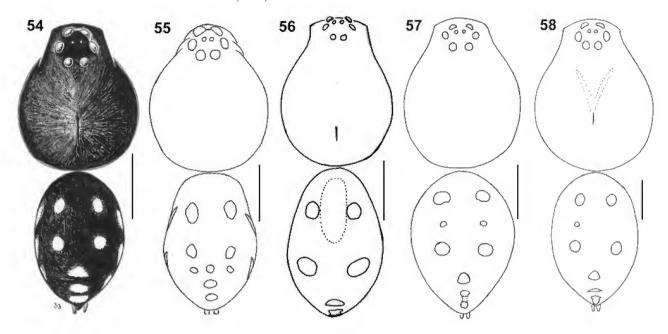
Female. Unknown.

**Distribution**. New South Wales (Fig. 139).

**Etymology**. Species name is an adjective taken from the type locality.



Figs. 51–53. Leg structures of *Habronestes* spp. (51–52) *Habronestes bradleyi* (Pickard-Cambridge): (51) claw with onychium, (52) tibia I proventral view, showing two rows of short feathery spines ventrally; (53) *Habronestes pseudoaustraliensis* n.sp., first tarsus (left side) with two rows of short ventral spines.



Figs. 54–58. Habronestes pictus species-group body, dorsal view: (54) Habronestes monocornis n.sp.; (55) Habronestes bicornis n.sp.; (56) Habronestes jocquei n.sp.; (57) Habronestes raveni n.sp.; (58) Habronestes giganteus n.sp. Scales 1 mm.

# Habronestes pictus species-group

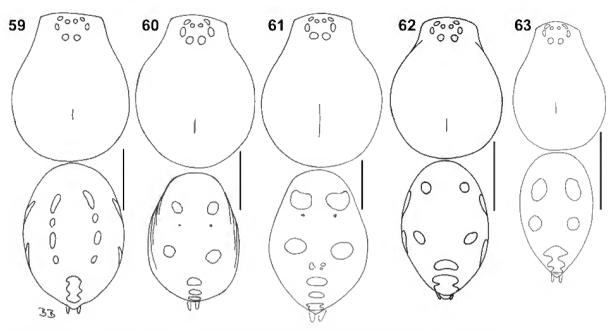
**Diagnosis.** Carapace not raised in front; AME or PME never largest eyes. Eyes in 2 rows, both rows procurved or in circular group. All eyes nearly equal-sized or AME smallest. Abdomen dark brown with 2–5 pairs of white patches on top, and 1–3 patches in front of spinnerets.

**Description**. *Male* (AM KS55869). Small to medium sized spiders (2.5–10.5) long. *Colour*. Carapace, sternum and chelicerae sepia brown or orange; maxillae, labium sepia brown, distally white. Abdomen sepia brown with 2–5 pairs of white patches on top and 1–3 patches in front of spinnerets; laterally with 1or 2 undulating horizontal white stripes; ventrally, 1 longitudinal white stripe from epigastric fold to near tracheal spiracle or none. Legs yellow or pale brown; clearly annulated or with indistinct colour pattern. *Carapace*. Oval; finely reticulated; with lateral rim and longitudinal fovea. *Sternum*. Heart-shaped anteriorly

straight; with lateral rim, no lateral extensions; finely striated; with short and longer setae. Eyes. All eyes nearly equal-sized or AME smallest. In 2 rows each with 4 eyes, both rows procurved or circular around AME. *Mouthparts*. Chelicerae, without teeth but with rows of hairs, bordering mesial margin, dorsally with a few hairs and bristles, laterally with condyle. Maxillae triangular, with promarginal scopula and without serrula; labium triangular. Abdomen. Oval; with ordinary short hairs; ALS on common base, conical, with very short distal segment; PLS small, widely spaced with PMS in one row; PMS tiny; colulus tiny with some hairs. Tracheal spiracle small slit-like, with sclerotized cover. Legs. Length formula 4123; 3rd claw on onychium (Fig. 51). Male palp (Figs. 1, 2). RCF deep, 3/3 to whole of cymbium length. LTA with long vertical stalk and irregular horizontal plate; DTA with flattened or thin stalk and curled apical end covered with spicules; VTA sickle-shaped, long, with sharp or blunt tip; embolus thin and semicircular. Tibiae short with DTiA and VTiA.

# Key to species of *H. pictus* species-group of New South Wales

1	Males
	- Females
2	Tibia I with 2 rows of short, feathery spines or with a band of short spines ventrally (Figs. 52)
	- Tibia I without special spines ventrally
3	Carapace orange iridescent. Tibia I with 2 rows of short, feathery ventral spines (Figs. 52). Palpal tibia without dorsolateral apophysis (Figs. 70, 71, 98)
	- Carapace dark brown. Tibiae and metatarsi I, II with a band of short spines ventrally
4	Cymbium laterally with conical spines. Metatarsus I with short, conical spines ventrally. Abdomen with 2 pairs of white patches and small scutum dorsally (Figs. 56, 68, 69)
	- Cymbium without conical spines. Abdomen with 3 pairs of white patches (Figs. 65, 72, 73, 110)



Figs. 59–63. Habronestes pictus species-group body, dorsal view: (59) Habronestes helenae n.sp.; (60) Habronestes grayi n.sp.; (61) Habronestes longiconductor n.sp.; (62) Habronestes minor n.sp.; (63) Habronestes wilkiei n.sp. Scales 1 mm.

5	Body length less than 3.8 mm, carapace less than 1.7 mm (Figs. 62, 63, 66)	6
	- Body length more than 4.5 mm, carapace more than 2.2 mm (Figs. 54, 55, 57–61, 64, 67)	8
6	Cymbium bent, RCF reaches to tip of cymbium (Figs. 62, 84, 85, 103)	H. minor
	- RCF not as long as cymbium (Figs. 83–86)	7
7	With extremely dorsally long DTiA, retrolateral part of LTA points to tip of cymbium (Figs. 66, 80, 81, 100)	H. piccolo
	- Without dorsally elongate DTiA, retrolateral part of LTA points to base of cymbium (Figs. 63, 82, 83, 105)	H. wilkiei
8	Eyes, AME smallest, others equal-sized (Figs. 54–61)	9
-	- Eyes equal-sized or AME and ALE smallest (Figs. 64–67)	
9	Eyes in circular group around AME (Figs. 54–58)	10
	- Eyes in 2 rows each with 4 eyes, both rows procurved (Figs. 59–61)	
10	Cymbium extremely bent, RCF reaches to the tip of cymbium. Embolus originates retrolaterally (Figs. 58, 96, 97, 106). Carapace orange brown	H. giganteus
	- Cymbium not extremely bent, RCF about ¾ of cymbium length. Embolus originates ventrally (Figs. 77–82). Carapace dark brown	11
11	VTA partly hidden by LTA. Without deep excavation between DTiA and VTiA (Figs. 78, 79, 109)	H. raveni
	- VTA free, visible. Deep excavation between DTiA and VTiA (Figs. 77–80)	12
12	Abdomen with 3 pairs of white patches dorsally. DTiA basally longer than tibia. LTA retrolaterally with 2 horns (Figs. 55, 74, 75)	H. bicornis
	- Abdomen with 2 pairs of white patches dorsally. DTiA basally not longer than tibia. LTA retrolaterally with 1 horn (Figs. 54, 76, 77)	

13	Cymbium extremely bent, RCF reaches to tip of cymbium. (Figs. 94, 95, 110)	H. longiconductor
	- Cymbium not extremely bent, RCF shorter than cymbium (Figs. 86, 87, 90, 91)	14
14	Palpal DTiA extremely long, twice as long as tibia. LTA retrolaterally with wings and bifurcate. VTA hidden by LTA. Abdomen with 2 pairs of white patches dorsally (Figs. 60, 90, 91, 99)	H. grayi
	86, 87, 104)	H. helenae
15	Abdomen with 5 pairs of white dots, 3 long and 2 small pairs dorsally. AME and ALE smallest. LTA with retrolateral tip pointed medially (Figs. 67, 92, 93, 108)	H. pictus
	- Abdomen with 2 pairs of white patches, dorsally. All eyes about equal size. LTA with retrolateral tip pointed outwards (Figs. 64, 90, 88, 89, 89a, 102)	H. grahami
16	(Females) Carapace orange iridescent, epigyne (Figs. 113, 114)	H. bradleyi
	- Carapace dark brown, epigyne different (Figs. 111, 112, 118–140)	ř
17	Body length less than 3.8 mm, carapace less than 1.7 mm (Figs. 62, 63, 66)	18
	- Body length more than 4.5 mm, carapace more than 2.2 mm (Figs. 54, 55, 57–61, 64, 67)	
18	Epigyne with long lanceolate scape (Figs. 121, 122)  - Epigyne without lanceolate scape (Figs. 123–126)	
19	Epigyne with sausage-like spermathecae in heart-shaped pattern visible through the tegument (Figs. 123, 124)	H. wilkiei
	- Epigyne with small v-shaped plate posteriorly. Vulva with long, spiralled copulatory ducts ending in large spermathecae (Figs. 125, 126)	H minor
20	AME smallest, others equal sized (Figs. 54–61)	
	- Eyes equal sized or AME and ALE smallest (Figs. 64–67)	
21	Eyes in circular group around AME (Figs. 54–58)	22
	Eyes in 2 rows each with 4 eyes, both rows procurved (Figs. 59–61)	
22	Epigyne with central opening at posterior margin. Vulva with kidney-shaped, medially touching copulatory ducts, ending in globular spermathecae (Figs. 119, 120)	H. raveni
	- Epigyne with large paired halfmoon-shaped openings. Vulva with s-shaped copulatory ducts (Figs. 111, 112, 117, 118)	23
23	Epigyne, large paired halfmoon-shaped plates touching medially (Figs. 111, 112)	H. jocquei
	- Epigyne, large paired halfmoon-shaped plates not touching medially (Figs. 117, 118)	H. monocornis
24	Abdomen with 4 pairs of white patches dorsally. Posterior margin of epigyne sinuous (Figs. 59, 127, 128)	H. helenae
	of epigyne not sinuous (Figs. 63, 64, 65, 115, 116, 129–132, 136, 137)	25
25	Epigyne medial with small inverted lanceolate hook. Copulatory ducts visible through tegument, anteriorly not touching (Figs. 136, 137)	H. longiconductor

	- Epigyne medial without lanceolate hook. Copulatory ducts visible through tegument anteriorly almost touching (Figs. 131, 132)
26	Abdomen with line of 5 pairs of white patches dorsally. Epigyne plate w-shaped (Figs. 67, 133–135)
	- Abdomen with only 2–3 pairs of white patches dorsally. Epigyne plate not w-shaped (Figs. 64, 65, 115, 116, 129, 130)
27	Abdomen with a line of 3 pairs of white patches dorsally. Epigyne with extremely separate small semicircular openings posteriorly (Figs. 65, 115, 116)
	- Abdomen with a line of 2 pairs of white patches dorsally. Epigyne, with inverted v-shaped scape (Figs. 64, 129, 130)

# Habronestes bradleyi (Pickard-Cambridge, 1869)

Figs. 1, 2, 51, 52, 70, 71, 98, 113, 114, 140

Storena bradleyi Pickard-Cambridge, 1869: 56, pl. 4, fig. 12–20 (description male); Kritscher, 1956: 246 (description female). Habronestes bradleyi.–L. Koch, 1872: 305 (description male); Jocqué, 1995: 143, figs. 2a,b (description male).

New Material examined. NSW: 1♀ Taleeban Woodland, 33°57'42"S 146°26'52"E, 23–27.ii.1999, DD, QM S50865; 1♀, QM S50912; 1♂ Bungonia Caves area near Information Centre, 34°48'2"S 150°0'57"E, xi.1989, on surface, Oct–Nov 1989, G. Hunt, AM KS22566; 19♂ ♂ Mt Lambie, 33°27'S 149°59'E, 13.xi.1988, road verge, G.S. Hunt, AM KS29940; 1♂ Rivatts Creek, Springwood, 33°38'S 150°40'E, 24.ii.1968, A. Speechley, AM KS1567; 1♀ Currawong, 34°28'S 148°22'E, 25.ix.1966, AM KS15678; 2♀♀ 1♂ 2.x.1966, plus ant prey, AM KS15682; 4♀♀ 2♂ ♂ Enfield, 33°53'S 151°6'E, 22.ix.1904, E.P. Ramsay, AM KS15558; 1♀ Goulburn, 34°45'S 149°43'E, 26.x.1898, J.A. Thorpe, AM KS15550; 1♀ Karuah SF, 0.1 km W along Hobart Forest Rd from Foleys Rd, 32°35'12"S 151°55'14"E, 4.ii–9.iv.1993, G/C, AM KS39431.

Remarks. Jocqué (1995) identified the material from the AM as *H. bradleyi* (AM KS20238) and *H. grimwadei* (AM KS29940, AM KS22566) and presented palpal drawings of both. Re-examination of the specimens did not reveal any differences in palp and body structure, which was confirmed by M. Gray and M. Zabka (pers. comm.). In contrast the holotype male from WA (40 mi W of Eucla, 30.8.1947, R.T.M.P. (Grimwade Exped.). (NVM K-113) (examined) and paratype: 1\$\forall \text{(NVM K-114)}\text{ (examined)}\text{ described from Dunn as *Storena grimwadei* Dunn, 1951: 11, figs. 1–4 (descriptions male and female) is a different species. Hence, the specimens of AM KS29940, AM KS22566 are identified as *H. bradleyi*.

**Diagnosis.** Carapace orange, blue iridescent. Eyes in 2 rows, both rows procurved, PME and PLE largest. Abdomen with 2 pairs of white patches on anterior part, the first small, the second long and 1 long white stripe in front of spinnerets. Tibia I with 2 rows of feathery spines proventrally. LTA with a long broad horizontal stalk and bilateral wings retrolaterally, which is similar to *H. grayi* n.sp.

**Description**. *Male*. Total length 4.52; carapace 2.32 long, 1.88 wide; 1.00 high; cl/cw 1.23; sternum 1.04 long, 1.00 wide; sl/sw 1.04. Abdomen 2.2 long, 1.64 wide. *Colour*. Carapace orange, blue, iridescent with dark fovea and dark bifurcate patches in front; sternum orange brown, iridescent; chelicerae yellow orange; maxillae and labium yellowish orange, distally white. Abdomen sepia brown, blue iridescent with 2 pairs of white patches on anterior part, first small, second long and 1 long, white stripe in front of spinnerets; laterally with 1 long, horizontal white stripe reaching front. Legs yellow, iridescent; with indistinct

colour pattern; legs I–IV with pale coxa, prolateral suture brownish, medium brown trochanter, medium brown femur; with darker brown lateral stripes on patella and tibia. Eyes. In 2 rows each with 4 eyes, both rows procurved. PME largest and PLE largest. Eye group width 0.45 of headwidth; AME 0.08; ALE 0.08; PME 0.12; PLE 0.12; AME-AME 0.06; AME-ALE 0.06; ALE-PLE 0.06; PME-PME 0.10; PME-PLE 0.10. MOQ: AME-PME 0.40; AME-AME 0.22; PME-PME 0.34. Clypeus & chilum. clypeus 0.56 high; chilum undivided, short. Legs. Length formula 4312; femora I-II with 1 row, femora III-IV with 2 rows of long, thin setae ventrally; tibia and metatarsus I with 2 rows of short, feathery spines proventrally (Fig. 52); Male palp (Figs. 1, 2, 70, 71, 98). RCF deep, almost running the entire cymbium length, with 3 strong spines apically; tegulum: LTA with a long broad horizontal stalk and bilateral wings retrolaterally; DTA with a thin stalk (Fig. 1); VTA with sharp tip. Tibiae short; VTiA (Fig. 71).

Female (QM S50865). Total length 5.50; carapace 2.66 long, 2.08 wide; 1.12 high; cl/cw 1.28; sternum 1.20 long, 1.12 wide; sl/sw 1.07. Abdomen 2.83 long, 2.50 wide. Colour. Same as male. Eyes. As in male. Eye group width 0.49 of headwidth; AME 0.10; ALE 0.10; PME 0.14; PLE 0.14; AME-AME 0.04; AME-ALE 0.08; ALE-PLE 0.08; PME-PME 0.12; PME-PLE 0.12. MOQ: AME-PME 0.40; AME-AME 0.24; PME-PME 0.40. Clypeus 0.8 high. Legs. Same as male except tibia and metatarsus I without feathery spines. Epigyne. With oval to semicircular opening. Vulva with long, spiralled copulatory ducts ending in spermathecae with parallel axis (Figs. 113, 114).

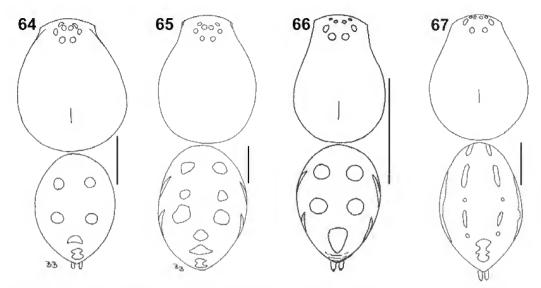
**Distribution**. New South Wales (Fig. 140), Victoria, Western Australia, Queensland.

# Habronestes bicornis n.sp.

Figs. 55, 74, 75, 142

**Type material**. HOLOTYPE ♂: NSW, Wilganea Station 5.5 km NW of homestead 90 km N of Bourke, 29°21'16"S 146°16'59"E, 13.iii.1993, open woodland, Mulga, Bimblebox, Silverleafed Ironbark, 9–16 Mar 1993, L. Gibson, AM KS83933. PARATYPES, all same data as holotype: 5 ♂ ♂ AM KS45257, 1 ♂ QM S60826, 1 ♂ AM KS45258, 1 ♂ AM KS45259, 4 ♂ ♂ AM KS45264.

**Diagnosis**. Eyes in circular group around AME, AME smallest, other eyes subequal. Abdomen with 3 pairs of white patches on anterior part and 3 or 4 patches in front of spinnerets. Palp, DTiA basally longer than tibia. LTA retrolaterally with 2 horns.



Figs. 64–67. Habronestes pictus species-group body, dorsal view: (64) Habronestes grahami n.sp.; (65) Habronestes hunti n.sp.; (66) Habronestes piccolo n.sp.; (67) Habronestes pictus (Koch). Scales 1 mm.

**Description**. *Male* (holotype). Total length 4.92; carapace 2.56 long, 2.00 wide; 1.08 high; cl/cw 1.28; sternum 1.20 long, 1.04 wide; sl/sw 1.15. Abdomen 2.36 long, 1.68 wide. Colour. Carapace sepia brown, iridescent; sternum sepia brown; chelicerae medium brown; maxillae and labium medium brown, distally white. Abdomen sepia brown with 3 pairs of white patches on anterior part and 3 or 4 patches in front of spinnerets; laterally with 2-3 long and broad white patches. Legs medium brown; clearly annulated; leg I, as legs II-IV but sepia brown femur; legs II-IV, white coxa, distally sepia brown, sepia brown trochanter, proximal 1/3-1/2 of femora white and distally sepia brown with darker brown lateral stripes on patella and tibia. Eyes. In circular group around AME. AME smallest, other eyes equal. Eye group width 0.68 of headwidth; AME 0.10; ALE 0.18; PME 0.18; PLE 0.18; AME-AME 0.04; AME-ALE 0.08; ALE-PLE 0.10; PME-PME 0.06; PME-PLE 0.10. MOO: AME-PME 0.44; AME-AME 0.24; PME-PME 0.42. Clypeus & chilum. Clypeus 0.52 high; chilum undivided, long. Legs. Length formula 4123; femora I, II with 1 row, femora III, IV with 2 rows of long, thin setae ventrally. *Male palp* (Figs. 74, 75). RCF deep, <sup>3</sup>/<sub>3</sub> cymbium length, cymbium with weak dorsal scopula and 4 strong spines apically; LTA with a thick, short vertical stalk, an irregular horizontal plate and 2 horns retrolaterally; DTA with a thin stalk; VTA broad, with sharp tip. Tibia short; DTiA large, basally longer than tibia, directed proximally with extremely deep concavity; VTiA (Fig. 75).

Female. Unknown.

**Distribution**. Known only from type locality in northwestern New South Wales (Fig. 142).

**Etymology**. Species name is chosen because of the two horns on the retrolateral part of the LTA in the male palp.

# Habronestes giganteus n.sp.

Figs. 58, 96, 97, 106, 140

**Type material**. HOLOTYPE ♂: NSW, Round Hill, Euabalong, 32°58'S 146°9'E, 15.v.1969, in gum litter, running by day (dull damp), M.R. Gray, AM KS50265. PARATYPES same data as holotype: 1♂ AM KS50264; 1♂ as previous but coll. 13.v.1972, AM KS50257.

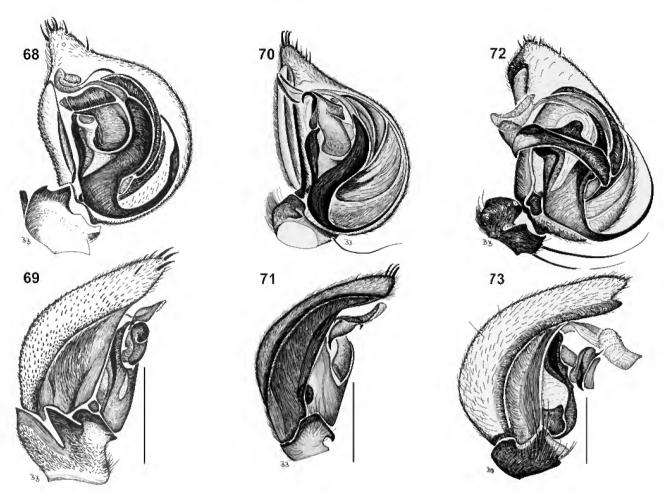
**Diagnosis**. Eyes in circular group around AME; AME smallest, other eyes subequal. Carapace orange brown. Abdomen with 2 pairs of white patches on anterior part and 3 patches in front of spinnerets. Big palp, cymbium extremely bent, RCF reaches over tip, similar to *H. longiconductor* but differs by shape of LTA.

**Description**. *Male* (holotype). Total length 6.84; carapace 3.68 long, 2.84 wide; 1.64 high, cl/cw 1.29; sternum 1.76 long, 1.56 wide, sl/sw 1.13. Abdomen 3.16 long, 3.28 wide. Colour. Carapace orange brown with dark fovea and dark bifurcate patches in front; sternum orange brown; chelicerae reddish brown; maxillae and labium medium brown, distally white. Abdomen sepia brown with 2 pairs of white patches on anterior part and 3 patches in front of spinnerets; laterally with 2 long white patches equal in length; ventrally with 1 longitudinal white stripe from epigastric fold to near tracheal spiracle. Legs orange brown; clearly annulated; legs I–IV with white coxa, proximal and prolateral sepia brown, sepia brown trochanter, sepia brown femur; femur IV additionally at proximal 1/3 with a white ring. Eyes. In circular group around AME. AME smallest, other eyes subequal. AME 0.10; ALE 0.24; PME 0.18; PLE 0.26; AME-AME 0.10; AME-ALE 0.10; ALE-PLE 0.08; PME-PME 0.16; PME-PLE 0.10. MOQ: AME-PME 0.54; AME-AME 0.3; PME-PME 0.52. Clypeus & chilum. Clypeus 0.8 high; chilum divided. Legs. Length formula 4123; femora I, II with 1 row and femora III, IV with 2 rows of long, thin setae ventrally *Male palp* (Figs. 96, 97, 106). RCF deep, running the entire cymbium length; from lateral view cymbium extremely bent with weak dorsal scopula and 4 strong spines apically. LTA with long, vertical stalk and irregular, horizontal plate (Fig. 106); DTA with a thin stalk; VTA long, with sharp tip. Tibiae short, DTiA as long as VTiA (Fig. 97).

Female. Unknown.

**Distribution**. Known only from type locality in western New South Wales (Fig. 140).

**Etymology**. Species name refers to the extremely large palps of the species.



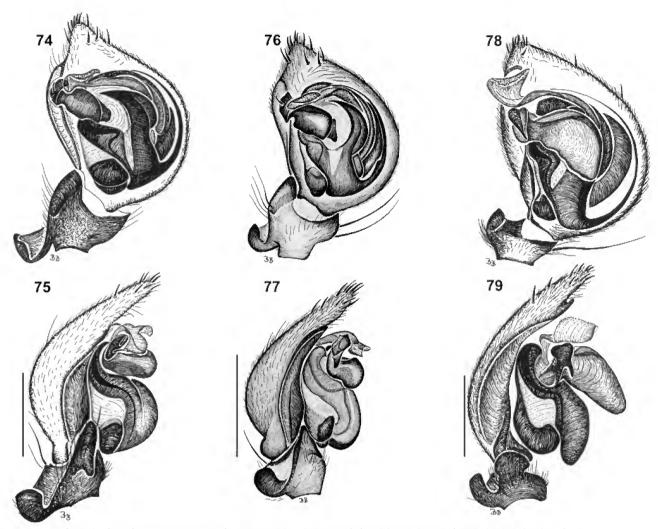
Figs. 68–73. *Habronestes pictus* species-group male palps, ventral view (above), lateral view (below): (68, 69) *Habronestes jocquei* n.sp.; (70, 71) *Habronestes bradleyi* (Pickard-Cambridge); (72, 73) *Habronestes hunti* n.sp. Scales 0.5 mm.

#### Habronestes grahami n.sp.

Figs. 64, 88, 89, 102, 129, 130, 140

Type material. HOLOTYPE of: NSW, Mount Brown Rd (0.1 km N from intersection at Mt Brown) 28°37'S 152°43'E, Richmond Range SF, 480 m, North East Forests Biodiversity Study (NSW NPWS) G/C, AM KS83929. PARATYPES: 1 as holotype, AM KS36027; 1  $\circlearrowleft$ , 1  $\circlearrowleft$ , 0.5 km from Wheatley Ck Rd on Camp Ck Rd, leasehold land, 28°47'0"S 152°19'29"E, 4.ii–9.iv.1993, 550 m, G/C, AM KS36270. 1♀, 2♂♂, 240 m E of inctn of Kunderang East & Kunderang West Rds, 30°48'53"S 152°2'9"E, 4.ii–9.iv.1993, 900 m, G/C, AM KS39106; 3♂♂ Barrington Tops SF, 1.3 km along Bungaree Trail from Barrington Tops Forest Rd, 31°56'44"S 151°21'9"E, 4.ii-9.iv.1993, 1180 m, G/C, AM KS39460; 23 & Beaury SF, Rocky Waterholes Rd, 28°32'49"S 152°20'11"E, 4.ii-9.iv.1993, 705 m, G/C, AM KS36148; 2♂♂ Bondi SF, S of Bombala, 37°8'S 149°9'E, 27.x.1980, Woodlot Survey, AM KS45436; 1 ♂ 25.x.1980, litter, open forest, WL1 DIV5, Woodlot Survey, G. Gowing et al., AM KS11003; 233 DIV3, further as previous, AM KS11007; 13 DIV 4, AM KS11025; 1♀ Boorook SF, 1 km E of main road, 28°49'20"S 152°11'14"E, 4.ii-9.iv.1993, 900 m, G/C AM KS36309; 1♀ Boundary Ck SF, SW along Boundary Ck Rd from jnctn of Dungel & Shannon Ck Rds, 29°56'48"S 152°33'27"E, 4.ii-9.iv.1993, 600 m, G/C, AM KS39030; 1 ♂ Bulga SF, Padmans Rd, nr intersection of Pole Dump Rd, 31°36'58"S 152°10'39"E, 4.ii-9.iv.1993, 730 m, G/C, AM KS39462; 1♀ Bulls Ground SF nr Wauchope, 31°33'S 152°38'E, 10.ii.1991, dry euc. open forest, Plot 6B3-burnt, 6-13 Feb 1991, A. York, NSW Forestry, AM KS43350; 2 ් ් Carrai SF, Block & Tackle Ridge, 500 m from Carrai Rd, 30°57'34"S 152°23'41"E, 4.ii-9.iv.1993, 540 m, G/C, AM KS39461; 1♂ Chaelundi SF, 1.2 km W along Stockyard from Chandlers Ck, 29°56'48"S 152°31'46"E, 4.ii–9.iv.1993, 450 m, G/C, AM KS39458; 1 ♂ Dorrigo NP, off Dorrigo-Bellingen Rd, about 20 km from Bellingen (to E of rd) about 500 m S of Newell Falls, 30°23'55"S 152°44'56"E, 4.ii–9.iv.1993, 410

m, G/C, AM KS35632; 2 & & East Kunderang Trail, 1.35 km E of West Kunderang Trail, 30°48'41"S 152°2'55"E, 4.ii-9.iv.1993, 890 m, G/C, AM KS55993; 2 of of Gilgurry SF, Rivertree Fire Trail, on ridge 2 km NNE from t/o, 28°45'18"S 152°15'52"E, 4.ii-9.iv.1993, 770 m, G/C, AM KS36247; 1& Glen Davis, 33°8'S 150°17'E, 31.v.1982, litter, 19 May-14 Jun 1982, B. Henke, AM KS10106; 3♀♀ Mt Hyland Nature Reserve, 1.9 km N on Chaelundi Rd from Big Bull Rd, 30°8'55"S 152°26'36"E, 4.ii-9.iv.1993, 1160 m, G/C, AM KS35614; 1♂ Mt Kosciusko, Island Bend, 36°19'S 148°29'E, 24.xi.1952, 455 m, J. Armstrong, AM KS15703; 2 d d Nadgee Nature Reserve, 37°22'S 149°55'E, 24.v.1978, in litter, 24 Feb-24 Jul 1978, G. Gowing, AM KS1610; 1♀ Ramornie SF, Mt Tindal Rd, 29°41'49"S 152°35'0"E, 4.ii-9.iv.1993, 490 m, G/C, AM KS39133; 1 ♀ Ramornie SF, track off Mt Tindal Rd, 29°42'41"S 152°37'36"E, 4.ii-9.iv.1993, 220 m, G/C, AM KS39130; 3 ♀ ♀ Ramornie SF, track off Mt Tindal Rd, 29°42'38"S 152°38'9"E, 4.ii-9.iv.1993, 200 m, G/C, AM KS39132; 2 ♀ ♀ Ramornie SF, T-ridge Rd, 29°43'13"S 152°33'38"E, 4.ii– 9.iv.1993, 300 m, G/C, AM KS39131; 1 ♂ Richmond Range SF, jnctn of Wattle Ck Rd and Wattle Ck, 28°38'9"S 152°46'40"E, 4.ii–9.iv,1993, 130 m, G/C, AM KS36044; 1 d Ridge between Camp Ck and Stydgy Ck, leasehold Land, 28°46'18"S 152°18'8"E, 4.ii-9.iv.1993, 640 m, G/C, AM KS36241; 2♂ ♂ Round Hill, Euabalong, 32°58'S 146°9'E, 13.v.1972, M.R. Gray, AM KS49141; 12, 13, Royal National Park, Sydney, 34°8'S 151°4′E, 22.vi.1969, R. Mascord, AM KS15683; 3♂♂ Stewarts Brook SF, 0.7 km W along unnamed logging track from Omadale Brook Rd, 31°54'16"S 151°23'36"E, 4.ii–9.iv.1993, 1250 m, G/C, AM KS39459; 19 Styx River SF off Cunnawarra Trail, about 2 km N Cunnawarra Ck, 30°32'49"S 152°20'16"E, 4.ii-9.iv.1993, 1070 m, G/C, AM KS35626; 2♂ ♂ Washpool NP, North West Fire Trail, 29°27'36"S 152°17'25"E, 4.ii– 9.iv.1993, 950 m, G/C, AM KS36406; 23 & Washpool NP, North West Fire Trail, 29°27'30"S 152°16'52"E, 4.ii-9.iv.1993, 950 m, G/C, AM KS36417; 1 ♂ 20 km N of Burcher on road to Manna Mountain, 33°22'12"S 147°15'2"E, 25.iii.1996, roadside corridor vegetation N5 trap B1, 21-28 Mar 1996, D. Smith & R. Harris, AM KS56121; 1♂ Booti



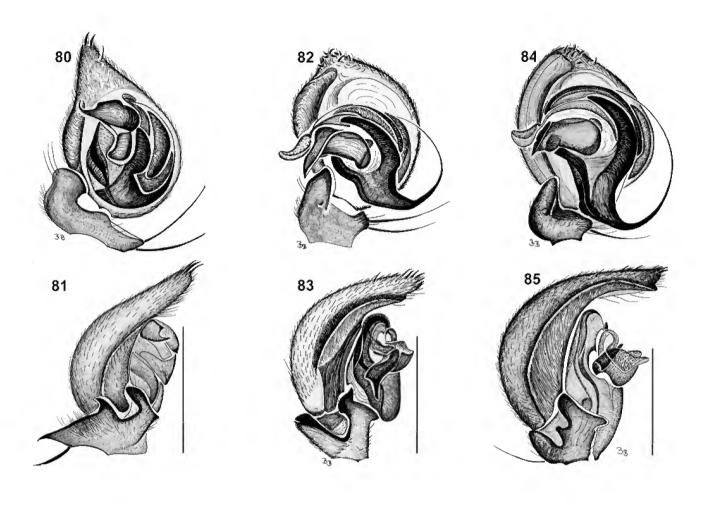
Figs. 74–79. *Habronestes pictus* species-group male palps, ventral view (above), lateral view (below). (74,75) *Habronestes bicornis* n.sp.; (76,77) *Habronestes monocornis* n.sp.; (78,79) *Habronestes raveni* n.sp. Scales 0.5 mm.

Booti NP, 32°16'15"S 152°31'42"E, 25.xi.1997, L. Wilkie, AM KS55939;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$ , AM KS55953;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$ , as previous, AM KS55959;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  as previous but 13.xii.1996, AM KS55968;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  Mummel Forest Rd, 7.6 km N of Enfield Forest Rd, Enfield SF, 31°17'S 151°51'E, 9.iv.1993, 1340 m, G/C, AM KS56063;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  Myall Lakes NP, 32°29'22"S 152°23'53"E, 13.iv.1998, L. Wilkie, AM KS56108;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  as previous, AM KS56109;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  as previous but 24.v.1998, AM KS56045;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  as previous, AM KS56043;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  Wyrrabalong NP, 33°16'44"S 151°32'51"E, 27.xi.1997, L. Wilkie, AM KS56011;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  Wyrrabalong NP, 33°16'47"S 151°32'40"E,2.v.1997, L. Wilkie, AM KS55933. The following in AM with same data as previous:  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  KS56036;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  KS56038;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  KS56118;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  15.iv.1998, KS55987;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  23.v.1998, KS56072;  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  AM KS56064. ACT:  $1\,\mbox{\ensuremath{\mathfrak{C}}}$  9 $\,\mbox{\ensuremath{\mathfrak{C}}}$  Tidbinbilla Nature Reserve, 35°28'S 148°52'E, 9.iii.1978, PO ref site 11, P. Ormay, AM KS13834.

**Diagnosis.** Eyes equal-sized, in 2 rows each with 4 eyes, both rows procurved. Abdomen with 2 pairs of white patches on anterior part and 1 or 2 patches in front of spinnerets. LTA with a thick, short vertical stalk and irregular horizontal plate, bird head shape retrolaterally. Epigyne with scape originating from central opening at posterior margin.

**Description**. *Male* (holotype). Total length 5.20; carapace 2.84 long, 2.20 wide; 0.96 high; cl/cw 1.29; sternum 1.24 long, 1.04 wide; sl/sw 1.19. Abdomen 2.36 long, 1.80 wide. *Colour*. Carapace, sternum sepia brown, iridescent; chelicerae reddish brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 2 pairs of white

patches on anterior part and 2 patches in front of spinnerets (Fig. 67); laterally with 2 long white patches equal in length; ventrally with 1 longitudinal white stripe from epigastric fold to near tracheal spiracle. Legs orange brown; clearly annulated; legs I-IV with white coxa, prolateral suture sepia brown, medium brown trochanter, proximal margin of femora sepia brown, proximal 1/2 white and distal 1/2 sepia brown, darker brown lateral stripes on patella and tibia; femur I with u-shaped pattern. Eyes. In 2 rows each with 4 eyes, both rows procurved. Nearly equal-sized. Eye group width 0.50 of headwidth; AME 0.12; ALE 0.12; PME 0.13; PLE 0.13; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.04; PME-PME 0.06; PME-PLE 0.10. MOQ: AME-PME 0.38; AME-AME 0.28; PME-PME 0.32. Clypeus & chilum. Clypeus 0.72 high; chilum undivided short. Abdomen. Oval; with stout bristles in front of tracheal spiracle. Legs. Length formula 4123; femora I, II with 1 row and femora III, IV with 2 rows of long thin setae ventrally. *Male palp* (Figs. 88, 89, 89a, 102). RCF deep, almost running the entire cymbium length; cymbium with a few strong spines apically. LTA with a thick, short, vertical stalk and irregular horizontal plate; DTA with a thin stalk; VTA sickle-shaped, long, with sharp tip. Tibiae short; DTiA with sharp tip, as long as tibia; VTiA (Fig. 89).



Figs. 80-85. Habronestes pictus species-group male palps, ventral view (above), lateral view (below): (80, 81) Habronestes piccolo n.sp.; (82, 83) Habronestes wilkiei n.sp.; (84, 85) Habronestes minor n.sp. Scales 0.5 mm.

Female (paratype AM KS35626). Total length 5.80; carapace 2.68 long, 1.72 wide; 1.08 high; cl/cw 1.20; sternum 1.20 long, 1.12 wide; sl/sw 1.07. Abdomen 3.12 long, 2.00 wide. Colour. Same as male. Eyes. Eye group width 0.51 of headwidth; AME 0.12; ALE 0.12; PME 0.14; PLE 0.14; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.04; PME-PME 0.06; PME-PLE 0.08. MOQ: AME-PME 0.34; AME-AME 0.28; PME-PME 0.34. Clypeus & chilum. Clypeus 0.6 high; chilum divided. Epigyne (Figs. 129, 130). With scape originating from central opening at posterior margin. Kidney-shaped and posteriorly touching copulatory ducts are visible through the tegument. Vulva with long, spiralled copulatory ducts ending in oval, medially touching spermathecae.

**Variation**. Males of this widespread species show some variation in the shape of palpal tibial apophysis (Fig. 89a).

**Distribution**. Widespread in New South Wales and ACT (Fig. 140).

**Etymology**. Species name is a patronym in honour of Mr Graham Milledge, the collection manager of Arachnology at the Australian Museum, who provided valuable technical assistance during this project.

#### Habronestes grayi n.sp.

Figs. 60, 90, 91, 99, 131, 132, 140

**Type material.** Holotype  $\delta$ : NSW, Ramornie SF, track off Mt Tindal Rd, 29°42'41"S 152°37'36"E, 4.ii–9.iv.1993, 220 m, G/C, AM KS83931. PARATYPES:  $10\delta$   $\delta$  same data as holotype, AM KS39194;  $1\delta$  as previous, AM KS56167; 2  $\bigcirc$   $\bigcirc$   $\bigcirc$  Boundary Ck SF, 0.45 km along Boundary Ck Rd from jnctn of Dungel & Shannon Ck Rds, 29°56'48"S 152°33'27"E, 4.ii–9.iv.1993, 600 m, G/C, AM KS39193,  $1\delta$  as previous, QM S60827;  $13\delta$   $\delta$  Boundary Ck SF, 1 km N along Joebill Rd from Shannon Ck Rd, 29°56'13"S 152°33'12"E, 4.ii–9.iv.1993, 630 m, G/C, AM KS39196;  $\delta\delta$   $\delta$  Boundary Ck SF, Shannon Ck Rd, 29°57'18"S 152°35'37"E, 4.ii–9.iv.1993, 300 m, G/C, AM KS39197;  $1\delta$  Ramornie SF, track off Mt Tindal Rd, 29°43'1"S 152°38'24"E, 9.iv.1993, 4.ii–9.iv.1993, 110 m, G/C, AM KS56169;  $1\delta$  Ramornie SF, track off Mt Tindal Rd, 29°42'S 152°38'E, 9.iv.1993, 4.ii–9.iv.1993, G/C, AM KS56171;  $23\delta$   $\delta$  Ramornie SF, track off Mt Tindal Rd, 29°42'38"S 152°38'9"E, 4.ii–9.iv.1993, 200 m, G/C, AM KS39195.

**Diagnosis**. Eyes in 2 rows, both rows procurved, PME and PLE largest. Abdomen with 2 pairs of large white patches on top and 3 patches in front of spinnerets. Extremely long DTiA; LTA with a long, broad horizontal stalk and irregular plate with bilateral wings retrolaterally, similar to *H. bradleyi*. Epigyne with paired broad-oval openings.

**Description**. *Male* (holotype). Total length 6.88; carapace 3.60 long, 2.68 wide; 1.20 high; cl/cw 1.34; sternum 1.76

long, 1.48 wide; sl/sw 1.18. Abdomen 3.28 long, 2.28 wide. Colour. Carapace, sternum and chelicerae sepia brown; maxillae and labium sepia brown, distally white. Abdomen sepia brown with 2 pairs of large white patches and 3 patches in front of spinnerets; laterally with 2 long white patches equal in length; ventrally with 1 longitudinal white stripe from epigastric fold to near tracheal spiracle. Legs yellow brown; clearly annulated; legs I–IV with white coxa, sepia brown trochanter, proximal \(^2\)\_1/2 of femora white and distal part sepia brown, sepia brown patella; Eyes. In 2 rows each with 4 eyes, both rows procurved, AME smallest, other eyes equal. Eye group width 0.53 of headwidth; AME 0.16; ALE 0.18; PME 0.18; PLE 0.18; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.04; PME-PME 0.08; PME-PLE 0.10. MOQ: AME-PME 0.54; AME-AME 0.36; PME-PME 0.44. Clypeus & chilum. Clypeus 0.8 high; chilum divided. Legs. Length formula 4123; femora I, II with 1 row and III, IV with 2 rows of long thin setae ventrally. Male palp (Figs. 90, 91, 99). RCF deep almost running the entire cymbium length. LTA with a long broad horizontal stalk and irregular plate with bilateral wings retrolaterally; DTA with a flattened stalk; VTA, long, with sharp tip. Tibia short; DTiA twice as long as tibia; VTiA (Fig. 91).

Female (paratype AM KS39193). Total length 7.84; carapace 3.44 long, 2.32 wide; 1.20 high; cl/cw 1.48; sternum 1.60 long, 1.44 wide; sl/sw 1.10. Abdomen 4.40 long, 3.08 wide. *Colour*. Same as male. *Eyes*. AME smallest, other eyes equal. Eye group width 0.51 of headwidth; AME 0.14; ALE 0.18; PME 0.18; PLE 0.18; AME–AME 0.06; AME–ALE 0.04; ALE–PLE 0.06; PME–PME 0.08; PME–PLE 0.12. MOQ: AME–PME 0.54; AME–AME 0.34; PME–PME 0.44. Clypeus 0.8 high. *Epigyne* (Figs. 131, 132). With paired broad-oval openings. Copulatory ducts anteriorly visible through the tegument. Vulva with long, spiralled copulatory ducts ending in pear-shaped, posteriorly touching spermathecae.

**Distribution**. Northeastern New South Wales (Fig. 140).

**Etymology**. The species name is a patronym honouring Dr Michael Gray of the Australian Museum, in esteem for his important work on Australian spiders.

### Habronestes helenae n.sp.

Figs. 59, 86, 87, 104, 127, 128, 141

**Type material.** HOLOTYPE &: NSW, Dipper Rd, Pilliga Nature Reserve, 30°40'S 148°50'E, 26.iii.1997, H. Smith & R. Harris, AM KS83935. PARATYPES: 1♀ same data as holotype, AM KS55696; 1 & Munmorah Recreation Reserve, Geebung camping area, 33°13'S 151°34'E, 3.iv.1987, M.R. Gray, AM KS17134.

**Diagnosis**. Eyes in 2 rows, both rows procurved, AME smallest, other eyes subequal. Abdomen with 4 pairs of white patches and 1 long patch in front of spinnerets. LTA massive. Epigyne with paired circular openings.

**Description**. *Male* (holotype). Total length 5.24; carapace 2.72 long, 2.00 wide; 1.32 high; cl/cw 1.36; sternum 1.24 long, 1.12 wide; sl/sw 1.11. Abdomen 2.52 long, 1.76 wide. *Colour*. Carapace chestnut brown; sternum pale yellow brown; chelicerae medium brown; maxillae and labium pale brown, distally white. Abdomen sepia brown, iridescent; with 4 pairs of white patches on top and 1 long patch in front of spinnerets; laterally pink brown with 2–3 long and

broad white patches; ventrally pale pink brown. Legs yellow brown; clearly annulated; leg I with white coxa, distal angles sepia brown, sepia brown trochanter, sepia brown femur, darker brown lateral stripes on patella and tibia, proximal half of tibiae white. Legs II-IV same except proximal 1/3 of femora II white and distal 3/3 sepia brown with proximal 1/2 of femora III, IV white and distal ½ sepia brown. Eyes. In 2 rows each with 4 eyes, both rows procurved. AME smallest, other eyes subequal. Eye group width 0.52 of headwidth; AME 0.12; ALE 0.14; PME 0.14; PLE 0.14; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.06; PME-PME 0.08; PME-PLE 0.10. MOQ: AME-PME 0.40; AME-AME 0.28; PME-PME 0.34. Clypeus & chilum. Clypeus 0.6 high; chilum undivided, short. Legs. Length formula 4123; femora I, II with 1 row II, IV with 2 rows of long, thin setae ventrally. Male palp (Figs. 86, 87, 104). RCF deep 3/4 of the cymbium length; cymbium with a few strong spines apically; LTA with a thick, short vertical stalk, and an irregular horizontal plate. DTA with a thin, long stalk. VTA long, with sharp tip. Tibiae short; with 2 long prolateral setae; DTiA short rounded; VTiA (Fig. 87).

Female (paratype AM KS55696). Total length 6.48; carapace 2.88 long, 1.96 wide; 1.04 high; cl/cw 1.46; sternum 1.36 long, 1.28 wide; sl/sw 1.06. Abdomen 2.52 long, 1.76 wide. Colour. Same as male. Eyes. Eye group width 0.5 of headwidth; AME 0.12; ALE 0.16; PME 0.16; PLE 0.16; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.06; PME-PME 0.08; PME-PLE 0.14. MOQ: AME-PME 0.44; AME-AME 0.28; PME-PME 0.40. Clypeus 0.64 high. Epigyne (Figs. 127, 128). With paired circular openings. Copulatory ducts anteriorly visible through the tegument. Vulva with long, spiralled copulatory ducts ending in large, oval touching spermathecae.

**Distribution**. Near coastal to western New South Wales (Fig. 141).

**Etymology**. Species name is a patronym in honour of Ms Helen Smith of the Australian Museum, one of the collectors of the holotype.

# Habronestes hunti n.sp.

Figs. 65, 72, 73, 110, 115, 116, 141

Type material. HOLOTYPE &: NSW, East Kunderang Trail, 1.35 km E of West Kunderang Trail, 30°48'41"S 152°2'55"E, 4.ii-9.iv.1993, 890 m, G/C, AM KS83932. PARATYPES: same data as holotype: 1♀, 11♂♂, AM KS39157; 1♂ as previous, QM S60825; 15♂♂ Richmond Range SF, Mt Brown Rd, 0.1 km N from Y intersection, 28°37'56"S 152°43'18"E, 4.ii–9.iv.1993, 480 m, G/C, AM KS36026; 1♀, 25♂♂ 0.5 km from Wheatley Ck Rd on Camp Ck Rd, leasehold land, 28°47'0"S 152°19'29"E, 4.ii-9.iv.1993, 550 m, G/C, AM KS36268; 1♀, 9♂♂ 2.8 km from Wheatley Ck access Rd (on Camp Ck), leasehold land, 28°47'10"S 152°18'37"E, 4.ii–9.iv.1993, 435 m, G/C, AM KS36250; 5 ♂ ♂ 240 m E of jnctn of Kunderang East & Kunderang West Rds, 30°48'53"S 152°2'9"E, 4.ii–9.iv.1993, 900 m, G/C, AM KS39160; 3 ♂ ♂ 3.45 km along Wheatley Ck Access Rd on Camp Ck Rd, 28°47'16"S 152°18'56"E, 4.ii-9.iv.1993, 470 m, G/C, AM KS36262; 1 & Ballengarra SF, Cooperabung Range Rd, 1.1 km S of Narang Rd, 31°12'54"S 152°42'44"E, 4.ii-9.iv.1993, 200 m, G/C, AM KS39182; 7 & & Ballengarra SF, Cooperabung Range Rd, 4.5 km N of Narang Rd, 31°11'46"S 152°42'25"E, 4.ii-9.iv.1993, 90 m, G/C, AM KS39181; 1& Beaury SF Rocky Waterholes Rd, 28°33'12"S 152°19'45"E, 4.ii–9.iv.1993, 630 m, G/C, AM KS36096; 11 ♂ ♂ Boonoo SF, jnctn Woolool Wooloolni and Basket Swamp Rd, 28°55'49"S 152°8'21"E, 4.ii-9.iv.1993, 1070 m, G/C, AM KS36340; 1 & Boonoo SF, Timbarra Trig, 28°56'41"S 152°8'31"E, 4.ii-9.iv.1993, 1130 m, G/C, AM KS36346; 1♂ Boorook SF, 1 km NW Boorook Ck jnctn, on Conlongan Rd, Midway between Boorook Ck and Gilgurry Ck on Conlongan Rd,

28°51'24"S 152°11'27"E, 4.ii–9.iv.1993, 980 m, G/C, AM KS36323; 1 \, \, 4 ♂ ♂ Boorook SF, 300 m NW of Gilgurry Mt, 28°47'23"S 152°10'56"E, 4.ii-9.iv.1993, 980 m, G/C, AM KS36315; 14 ♂ Boundary Ck SF, 1.9 km along Sheas Nob Rd from Boundary Ck Rd, 29°59'25"S 152°34'33"E, 4.ii-9.iv.1993, 550 m, G/C, AM KS39022; 2♀♀, 16♂♂ Boundary Ck SF, 100 m S of inctn of Dilli & Boundary Ck Rds, 29°58'14"S 152°36′51″E, 4.ii–9.iv.1993, 540 m, G/C, AM KS39012; 3 ♂ ♂ Bulga SF, 1.2 km up 4WD track N of Grey Gums Forest Rd 2.1 km from Douglas River Rd, 31°32'56"S 152°14'51"E, 4.ii-9.iv.1993, 620 m, G/C, AM KS39186; 1♀, 3♂ ♂ Bulga SF, Grey Gums Forest Rd 1.1 km from Doyles River Rd, 31°33'35"S 152°14'36"E, 4.ii-9.iv.1993, 620 m, G/C, AM KS39187; 3  $\ensuremath{\,^\circ}$   $\ensuremath{\,^\circ}$  , 1  $\ensuremath{\,^\circ}$  Bulga SF, Padmans Rd nr intersection of Pole Dump Rd, 31°36'58"S 152°10'39"E, 4.ii-9.iv.1993, 730 m, G/C, AM KS39190; 1 ♀ Bulls Ground SF nr Wauchope, 31°33'S 152°38'E, 10.ii.1991, dry euc. open forest, Plot 3B4-burnt, 6-13 Feb 1991, A. York, NSW Forestry, AM KS43349; 1♂ Bundjalung NP, hilltop on ridge between Big Marsh & Esk River, 29°17'35"\$ 153°16'40"E, 4.ii-9.iv.1993, 23 m, G/C, AM KS39016; 4 d d Bundjalung NP, nr new gravel quarry, 29°17'12"S 153°16'40"E, 4.ii–9.iv.1993, 20 m, G/C, AM KS39017; 1♀, 12♂♂ Chaelundi SF, 1.2 km W along Stockyard FT from Chandlers Ck, 29°56'48"S 152°31'46"E, 4.ii–9.iv.1993, 450 m, G/C, AM KS39015; 9 ් ී Chaelundi SF, 3.8 km W along Stockyard FTfrom Chandler Ck, 29°57′50"S 152°31′23"E, 4.ii–9.iv.1993, 450 m, G/C, AM KS39025; 1 \, \, \ 1 ♂ Conglomerate SF, along new logging rd below dam, 0.55 km SW along Old Growth Rd, N side of rd, 30°6'55"S 153°4'55"E, 4.ii–9.iv, 1993, 380 m, G/C, AM KS39020; 1 ♂, as previous, AM KS48712; 3 ♀ ♀, 20 ♂ ♂ Conglomerate SF, 1.7 km NW on Murphys Rd from Madmans Ck Bridge, on S side of ridge, 30°3'57"S 153°5'58"E, 4.ii-9.iv.1993, 220 m, G/C, AM KS39013; 8 ♂ ♂ Conglomerate SF, 100 m SW of jnctn of Hallgraths Trail & Sherwood rd, 30°7'0"S 153°3'14"E, 4.ii-9.iv.1993, 320 m, G/C, AM KS39019; 2♀♀, 24♂♂ Conglomerate SF, 700 m N along Murphys Rd, from Tea Tree Rd, W side of rd, S of Madmans Ck, 30°4'52"S 153°6′24″E, 4.ii–9.iv.1993, 130 m, G/C, AM KS39023; 1♀ Dorrigo NP, off Dorrigo-Bellingen Rd, about 20 km from Bellingen (to E of rd) about 500 m S of Newell Falls, 30°23'55"S 152°44'56"E, 4.ii-9.iv.1993, 410 m, G/C, AM KS35631; 11 ♂ ♂ East Kunderang Trail, 2.1 km E of West Kunderang Trail, 30°49'0"S 152°3'25"E, 4.ii-9.iv.1993, 845 m, G/C, AM KS39161; 1& Enfield SF, Dodds Fire Trail, 1 km from Enfield Rd, 31°23'44"S 151°53'6"E, 4.ii-9.iv.1993, 1050 m, G/C, AM KS39159; 193 ♂ Enfield SF, Mummel Forest Rd, 7.6 km N of jnctn with Enfield Forest Rd, 31°17'0"S 151°51'17"E, 4.ii-9.iv.1993, 1340 m, G/C, AM KS39158; 1& Euroka, Blue Mountains, 33°45'S 150°13'E, 8.iii.1965, A.E. Speechley, AM KS15596; 17 & & Gilgurry SF, Rivertree Fire Trail, on ridge 2 km NNE from t/o, 28°45'18"S 152°15'52"E, 4.ii-9.iv.1993, 770 m, G/C, AM KS36245; 2♀♀, 56♂♂ Headwaters of Wheatley Ck, leasehold Land, 28°45'7"S 152°19'44"E, 4.ii-9.iv.1993, 550 m, G/C, AM KS36265; 1 & Kangaroo River SF, 200 m E of a point 550 m along Burns Rd, 30°4'36"S 152°52'5"E, 4.ii–9.iv.1993, 320 m, G/C, AM KS39021; 1 ♂ Kangaroo River SF, 700 m E of Arinya Rd on a logging track 900 m from Burns Rd inctn, 30°4'36"S 152°52'5"E, 4.ii-9.iv.1993, 360 m, G/C, AM KS39014; 3 ♂ ♂ Karuah SF, 0.1 km W along Hobart Forest Rd from Foleys Rd, 32°35'12"S 151°55'14"E, 4.ii-9.iv.1993, 10 m, G/C, AM KS39180; 15 3 3 Karuah SF, NE slope of Little Mountain, just W of Karuah Rd, 32°36'17"S 151°56'41"E, 4.ii-9.iv.1993, 40 m, G/C, AM KS39189; 2 む お Karuah SF, SE of jnctn Little Mtn & Hobart Forest Rds, 32°35'45"S 151°56'15"E, 4.ii−9.iv.1993, 10 m, G/C, AM KS39188; 1 ♂ Kirrawee, 34°2'S 151°4'E, 26.iii.1967, AM KS15677; 1♀, 17♂♂ London Bridge SF, 3.7 km SW of London Bridge Lookout, end of FC survey rd, off London Bridge Rd overlooking gorge, 29°51'31"S 152°12'47"E, 4.ii-9.iv.1993, 960 m, G/C, AM KS36393; 2 & & McPherson Range, 28°22'S 152°50'E, 23.ii.1989, hoop pine, Mt Warning Caldera Survey, UNE, 300 m, Smith, Hines, Pugh & Webber, AM KS55703; 3 \ \ \ \ \ \ , 30 \ \ \ \ Morgan Ck, 5.9 km NE from creek crossing, 28°46'31"S 152°18'45"E, 4.ii-9.iv.1993, 620 m, G/C, AM KS36256; 7 d d Morgans Ck, 4.5 km NE from creek crossing on Wheatley Ck Rd on Wheatley Ck access road, leasehold land, 28°46'37"S 152°18'19"E, 4.ii-9.iv.1993, 590 m, G/C, AM KS36259; 21 ♂ Nerang SF, 0.45 km E along Boundary Rd from Masonite Track, 32°32'16"S 152°7'40"E, 4.ii–9.iv.1993, 130 m, G/C, AM KS39185; 9 of o Nerang SF, 0.3 km S along Coxs Fence Trail from Boundary Rd, 31°38′19"S 152°9′30"E, 4.ii–9.iv.1993, 70 m, G/C, AM KS39184; 1♂ Oakwood SF, 0.3 km along Sydney Plain Hut Track from London Bridge Fire Trail, 29°55'25"S 152°5'58"E, 4.ii-9.iv.1993, 970 m, G/C, AM KS36383; 1♂ Oakwood SF, 0.65 km N along Oakwood FT from London Bridge Fire Trail, 29°53'45"S 152°5'41"E, 4.ii-9.iv.1993, 1060 m, G/C, AM KS36376; 2 d d Oakwood SF, 250 m upstream of London Bridge Fire Trail, House Ck, 29°54'23"S 152°5'25"E, 4.ii-9.iv.1993, 1000 m, G/ C, AM KS36374; 1 d Port Hacking, 34°4'S 151°7'E, 1.iii.1969, Mascord coll. no.490, N. Allen, AM KS15597; 21 & Ramornie SF, Main Ck, track

off Mt Tindal Rd, 29°43'1"S 152°38'24"E, 4.ii-9.iv.1993, 110 m, G/C, AM KS39480; 1♀, 31♂ Ramornie SF, Mt Tindal Rd, 29°42'12"S 152°35'26"E, 4.ii–9.iv.1993, 380 m, G/C, AM KS39483; 1♀, 11♂♂ Ramornie SF, Mt Tindal Rd, 29°41'49"S 152°35'0"E, 4.ii-9.iv.1993, 490 m, G/C, AM KS39484; 1♀, 25♂♂ Ramornie SF, track off Mt Tindal Rd, 29°42'41"S 152°37'36"E, 4.ii-9.iv.1993, 220 m, G/C, AM KS39481: 10 ♂ ♂ Ramornie SF, track off Mt Tindal Rd, headwaters of Valorem Ck, 29°42'18"S 152°35'52"E, 4.ii-9.iv.1993, 380 m, G/C, AM KS39482; 30 & Ramornie SF, track off T-Ridge Rd, 29°43'0"S 152°33'23"E, 4.ii-9.iv.1993, 150 m, G/C, AM KS39479; 1♀, 5♂♂ Ramornie SF, T-Ridge Rd, 29°43'23"S 152°34'11"E, 4.ii–9.iv.1993, 420 m, G/C, AM KS39477: 19, 21 & Ramornie SF, T-Ridge Rd, 29°43'13"S 152°33'38"E, 4.ii-9.iv.1993, 300 m, G/C, AM KS39478; 31 & Richmond Range SF, jnctn of Wattle Ck Rd and Wattle Ck, 28°38'9"S 152°46'40"E, 4.ii-9.iv.1993, 130 m, G/C, AM KS36045; 20♂ Richmond Range SF, Oaky Ck Rd, 28°38'39"S 152°45'45"E, 4.ii–9.iv.1993, 230 m, G/C, AM KS36050; 1 &, as previous, AM KS36052; 27 & Richmond Range SF, Wattle Ck Rd, 28°38'42"S 152°46'29"E, 4.ii–9.iv.1993, 220 m, G/C, AM KS36060; 5 ♂ ♂ Ridge between Camp Ck and Stydgy Ck, leasehold Land, 28°46'18"S 152°18′8″E, 4.ii–9.iv.1993, 640 m, G/C, AM KS36242; 1♂ St Georges Basin, 35°5'S 150°35'E, i.1984, I. Buddle, AM KS22639; 1♂ Styx River SF off Cunnawarra Trail, about 2 km N Cunnawarra Ck, 30°32'49"S 152°20'16"E, 4.ii-9.iv.1993, 1070 m, G/C, AM KS35627; 1♂ Tweed Range, 28°25'S 153°1'E, 16.ii.1989, wet sclerophyll, Mt Warning Caldera Survey, UNE, 400 m, Smith, Hines, Pugh & Webber, AM KS55699; 2♀♀, 25 ♂ ♂ Wallaroo SF, Flaggy Ck, 0.95 km S along Ripleys Trail from Clarence Town Rd, 32°36'3"S 151°48'7"E, 4.ii-9.iv.1993, 20 m, G/C, AM KS39183; 1033 Wallaroo SF, Gilmore Lookout, 32°37'27"S 151°47'16"E, 4.ii–9.iv.1993, 210 m, G/C, AM KS39191; 2♂♂ Washpool NP, North West Fire Trail, 29°27'36"S 152°17'25"E, 4.ii-9.iv.1993, 950 m, G/C, AM KS36405; 3 of d Washpool NP, North West Fire Trail, 29°27'30"S 152°16'52"E, 4.ii–9.iv.1993, 950 m, G/C, AM KS36418; 1 &, as previous, AM KS56168; 2♂♂ Washpool NP, Washpool Forest Way, 29°24'47"S 152°17'0"E, 4.ii-9.iv.1993, 860 m, G/C, AM KS36295; 1 & Bendoura SF, 700 m E of Wallaces Gap, 35°34'37"S 149°41'16"E, 16.iii.1999, J. Tarnawski & S. Lassau, AM KS55853; 1 d Dampier SF, Ross Rixon Rd, 36°2'56"S 149°57'21"E, 11.iii.1999, L. Wilkie, R. Harris & H. Smith, AM KS55854; 1 & Dampier SF, Ross Rixon Rd, 36°2'56"S 149°57'36"E, 11.iii.1999, L. Wilkie, R.Harris & H.Smith, AM KS55857; 1 ♂ Nerrigundah Mt Rd, Dampier SF, 36°7'58"S 149°56'2"E, 10.iii.1999, J. Tarnawski & S. Lassau, AM KS55855; 1♀ Rocky Waterholes Rd, Beaury SF, 28°32'S 152°20'E, 9.iv.1993, 4.ii-9.iv.1993, 705 m, G/C, AM KS56166; 1♂ Tobacco Pinch Rd, Bodalla SF, 36°10'55"S 150°2'56"E, 10.iii.1999, J. Tarnawski & S. Lassau, AM KS55856; 1♂ Tuross River Rd, Bodalla SF, 36°11'13"S 149°56'13"E, 10.iii.1999, L. Wilkie, R.Harris & H.Smith, AM KS55858; 1 & 7.5 km S of Nelligen, Mogo SF, 35°43'19"S 150°6'50"E, 8.iii.1999, J. Tarnawski & S. Lassau, AM KS55861; 1♂ Brou Lake Rd, Narooma, Site 3, 36°7'15"S 150°2'49"E, 9.iii.1999, L. Wilkie, R. Harris & H. Smith, AM KS55852; 13 Highway 54, 32 km NW of Batemans Bay, 35°33'7"S 149°59'38"E, 16.iii.1999, J. Tarnawski & S. Lassau, AM KS55870; 13 jnctn of Skid Ridge & North Head Rds, Murramarang NP, 35°41'9"S 150°16'4"E, 17.iii.1999, L. Wilkie, R. Harris & H. Smith, AM KS55862; 1♂ Orange Ridge Rd, Bodalla SF, 36°16′55"S 149°53'31"E, 12.iii.1999, L. Wilkie, R. Harris & H. Smith, AM KS55863; 1 ♂ Tuross River Rd, Bodalla SF, 36°10'51"S 149°56'41"E, 10.iii.1999, L. Wilkie, R. Harris & H. Smith, AM KS55859; 1 ♂ Tuross River Rd, Bodalla SF, 36°11'16"S 149°56'16"E, 10.iii.1999, L. Wilkie, R. Harris & H. Smith, AM KS55871; 1♂ Turtle Creek Fire Trail, Monga SF, 35°38'20"S 149°55'55"E, 15.iii.1999, L. Wilkie, R. Harris & H. Smith, AM KS55860.

**Diagnosis**. Eyes equal sized. Abdomen with 3 pairs of large white patches on anterior part and 3 patches in front of spinnerets. Tibiae and metatarsi I, II with irregular band of short spines ventrally in males. Extremely small DTiA, LTA with transverse plate.

**Description**. *Male* (holotype). Total length 7.56; carapace 3.72 long, 2.84 wide; 0.88 high; cl/cw 1.31; sternum 1.80 long, 1.56 wide; sl/sw 1.15. Abdomen 3.84 long, 2.48 wide. *Colour*. Carapace, sternum, chelicerae sepia brown; maxillae, labium sepia brown, distally white. Abdomen sepia brown with 3 pairs of white patches on anterior part and 3 patches in front of spinnerets; laterally with 2 long white patches equal in length; ventrally with 1 longitudinal white stripe from epigastric fold to near tracheal spiracle

and 1 pair of white patches near tracheal spiracle. Legs yellow; clearly annulated; legs I–IV with white coxa, sepia brown trochanter, proximal ½–½ of femora white and distal part sepia brown. Eyes. In 2 rows each with 4 eyes, both rows procurved. Nearly equal sized. Eye group width 0.51 of headwidth; AME 0.18; ALE 0.16; PME 0.18; PLE 0.18; AME–AME 0.04; AME–ALE 0.04; ALE–PLE 0.04; PME–PME 0.12; PME–PLE 0.16. MOQ: AME–PME 0.52; AME–AME 0.40; PME–PME 0.48. Clypeus & chilum. Clypeus 0.88 high; chilum divided. Legs. Length formula 4123; tibiae and metatarsi I, II with a band of short spines ventrally. Male palp (Figs. 72, 73, 110). RCF deep, almost running the entire cymbium length. LTA with a long vertical stalk, and T-shaped plate; DTA with a thin stalk; VTA with sharp tip. Tibiae short; DTiA short; VTiA (Fig. 73).

Female (paratype AM KS39013). Total length 10.1; carapace 4.29 long, 2.94 wide; 1.55 high; cl/cw 1.46; sternum 1.88 long, 1.76 wide; sl/sw 1.07. Abdomen 5.83 long, 3.50 wide. Colour. Same as male. Eyes. Eye group width 0.5 of headwidth; AME 0.19; ALE 0.20; PME 0.22; PLE 0.22; AME-AME 0.04; AME-ALE 0.06; ALE-PLE 0.08; PME-PME 0.16; PME-PLE 0.20. MOQ: AME-PME 0.58; AME-AME 0.42; PME-PME 0.60. Clypeus 1.02 high. Legs. Same as male, but without irregular band of short ventral spines on tibiae and metatarsi I, II. Epigyne (Figs. 115, 116). With small paired halfmoon-shaped copulatory openings laterally. Vulva with very large atrium-like copulatory ducts ending in almost touching spermathecae.

**Distribution**. Widespread in eastern New South Wales (Fig. 141).

**Etymology**. Species name is a patronym in honour of Dr Glenn Hunt of the Australian Museum, an experienced arachnologist, whose recent death was a great loss to Australian arachnology.

# Habronestes jocquei n.sp.

Figs. 56, 68, 69, 101, 111, 112, 141

**Type material**. HOLOTYPE &: NSW, between Condobolin & Euabalong, 33°6'S 146°50'E, iii.1972, under rock near edge of road, M.R. & G.E. Gray, AM KS83928. PARATYPES same data as holotype: 1♀, AM KS15656; 1♂ QM S60824.

**Diagnosis**. Eyes in circular group around AME, AME smallest, other eyes subequal. Abdomen with 2 pairs of white patches on anterior part and 2 patches in front of spinnerets. Tibia and metatarsus I with a band of conical, thorn-like spines ventrally; palpal tibia and cymbium with thick, thorn-like spines retrolaterally in males. Tibia III with a row of 4 stout dorsal spines at distal end, tibia IV with a row of 3 stout dorsal spines at distal end in females. Epigyne with large, paired halfmoon-shaped openings.

**Description**. *Male* (holotype). Total length 5.32; carapace 2.80 long, 2.00 wide; 0.76 high; cl/cw 1.40; sternum 1.24 long, 1.12 wide. Abdomen 2.52 long, 1.80 wide. *Colour*. Carapace chestnut brown, iridescent; sternum yellow brown; chelicerae medium brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 2 pairs of white patches on anterior part and 2 patches in front of spinnerets; laterally with 2 long white patches equal in

length; ventrally medium brown. Legs yellow brown with sepia brown femora and pale tibiae in proximal half, colour pattern indistinct. Eves. In circular group around AME. AME smallest, other eyes about equal-sized. Eye group width 0.52 of headwidth: AME 0.10: ALE 0.14: PME 0.12: PLE 0.13; AME-AME 0.04; AME-ALE 0.02; ALE-PLE 0.03; PME-PME 0.06; PME-PLE 0.10. MOQ: AME-PME 0.44; AME-AME 0.24; PME-PME 0.30. *Clypeus & chilum*. Clypeus 0.52 high; chilum undivided, long. Legs. Length formula 4123; tibia I with a band of conical, thorn-like spines ventrally; metatarsus I with 2 rows of thick, thornlike spines ventrally. Male palp (Figs. 68, 69, 101). RCF deep, 3/3 of the cymbium length; cymbium with thick, thornlike spines retrolaterally. LTA with a short vertical stalk and irregular plate; DTA with a thin stalk; VTA long, rounded at tip; tibia globose; with thick, thorn-like spines retrolaterally; DTiA triangular; VTiA (Fig. 69).

Female (paratype AM KS15656). Total length 6.80; carapace 3.10 long, 1.90 wide; 1.60 high; cl/cw 1.63; sternum 1.30 long, 1.16 wide. Abdomen 3.00 long, 1.88 wide. Colour. Same as male. Eyes. Eye group width 0.53 of headwidth; AME 0.10; ALE 0.16; PME 0.12; PLE 0.14; AME–AME 0.06; AME–ALE 0.03; ALE–PLE 0.04; PME–PME 0.08; PME–PLE 0.16. MOQ: AME–PME 0.44; AME–AME 0.28; PME–PME 0.34. Clypeus 0.56 high. Abdomen. Oval; with stout bristles in front of tracheal spiracle. Legs. Tibia III with a row of 4 stout, dorsal spines at distal end; tibia IV with a row of 3 stout, dorsal spines at distal end. Epigyne (Figs. 111, 112). With large, paired, halfmoonshaped openings. Vulva with s-shaped copulatory ducts ending in small separated spermathecae.

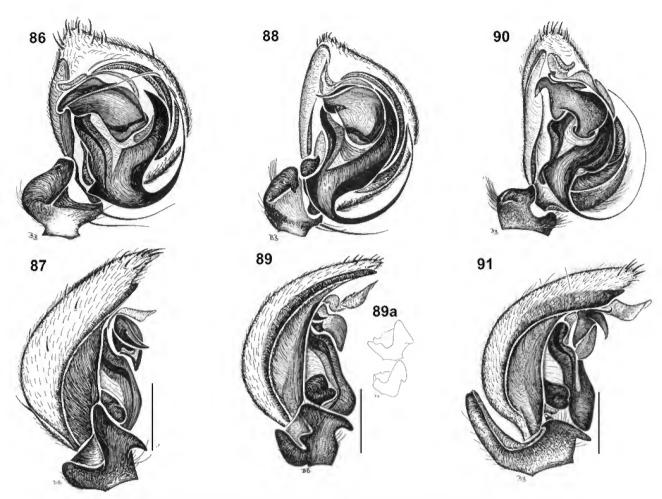
**Distribution**. Known only from the type locality in western New South Wales (Fig. 141).

**Etymology**. Species name is a patronym in honour of Dr Rudy Jocqué of the African Museum in Tervuren, a world expert in Zodariidae.

# Habronestes longiconductor n.sp.

Figs. 61, 94, 95, 107, 136, 137, 141

**Type material.** HOLOTYPE ♂: NSW, Corringle SF, 33°22'12"S 147°15'0"E, 25.iii.1996, Callitris forest F5 trap B3, 21–28 Mar 1996, D. Smith & R. Harris, AM KS49596. PARATYPES: 6 ♂ ♂ 20 km N of Burcher on rd to Manna Mtn, 33°22'12"S 147°15'2"E, 25.iii.1996, roadside corridor vegetation N5 Trap B1, 21-28 Mar 1996, D. Smith & R. Harris, AM KS49550; 188 d Gubatta, 33°32'0"S 146°31'28"E, 24–28.ii.1999, DD, QM S50823; 1♀, 5♂♂ as previous, QM S50834; 1♂ Gubatta, 33°38'10"S 146°33'8"E, 24–28.ii.1999, DD, QM S50876; 9& & Gubatta, 33°32'3"S 146°31'56"E, 24–28.ii.1999, DD, QM S50930; 12♂♂ as previous, QM S50943; 1♀, 22♂ ♂ Gubatta, 33°34'33"S 146°34'36"E, 24–28.ii.1999, DD, QM S50937; 2♀♀, 37♂♂ as previous, QM S51016; 4♂♂ Gubatta, 33°38'7"S 146°33'12"E, Pulletop, 34°0'6"S 146°5'10"E, 24–28.ii.1999, DD, QM S50993; 1♀, 15♂♂ as previous, QM S51517; 12, 12 of of Pulletop, 34°0'59"S 146°4'15"E, 24-28.ii.1999, DD, QM S51521; 19 & & as previous, QM S51573; 2 & & Pulletop, 33°58'55"S 146°4'46"E, 24–28.ii.1999, DD, QM S51588; 8 ♂ ♂ as previous, QM S51605; 1 & Round Hill, near Euabalong, 32°58'S 146°9'E, 4.v.1972, M.R. Gray, AM KS50263; 1& iii.1968, in Mallee leaf litter, AM KS15701; 1 d Taleeban Woodland, 33°56'29"S 146°25'8"E, 23–27.ii.1999, DD, QM S39854; 13 as previous, QM S50914; 12, 1233 Taleeban Woodland, 33°55'33"S 146°28'23"E, 23–27.ii.1999, DD, QM S50830; 7 & & as previous, QM S51597; 1& Taleeban Woodland, 33°57'42"S 146°26'52"E, 23-27.ii.1999, DD, QM S50843; 23 3 as previous, QM S50867; 23 3 Taleeban Woodland, 33°55′16″S 146°27′19″E, 23–27.ii.1999, DD, QM S50846; 18♂♂ as previous, QM S51627.



Figs. 86–91. Habronestes pictus species-group male palps, ventral view (above), lateral view (below): (86, 87) Habronestes helenae n.sp.; (88, 89) Habronestes grahami n.sp.; (90, 91) Habronestes grayi n.sp. Scales 0.5 mm.

**Diagnosis**. Eyes in 2 rows, both rows procurved, AME smallest, other eyes subequal. Abdomen with 2 pairs of large white patches and 3 patches in front of spinnerets. Palpal cymbium large and extremely bent, RCF reaches over tip; similar to *H. giganteus* but differs by shape of LTA and extremely long DTA. Epigyne with small, paired, half moon shaped openings and a medial lanceolate hook.

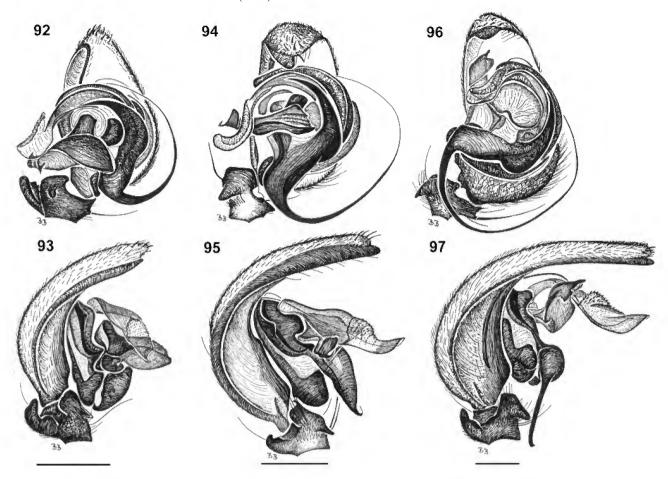
**Description**. *Male* (holotype). Total length 5.16; carapace 2.80 long, 2.16 wide; 1.16 high; cl/cw 1.30; sternum 1.36 long, 1.16 wide; sl/sw 1.17. Abdomen 2.36 long, 1.72 wide. Colour. Carapace sepia brown, iridescent; sternum yellow brown; chelicerae medium brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 2 large pairs of white patches and 3 patches in front of spinnerets; laterally with 2 long white patches equal in length; ventrally pink brown. Legs yellow brown; clearly annulated; legs I-IV with white coxa, prolateral suture sepia brown, sepia brown trochanter, proximal margin of femora sepia brown, proximal 1/2 white and distal 1/2 sepia brown, u-shaped pattern, sepia-brown lateral stripes on patella, tibiae and metatarsi. Eyes. In 2 rows each with 4 eyes, both rows procurved. AME smallest, other eyes equal. Eye group width 0.53 of headwidth; AME 0.12; ALE 0.14; PME 0.16; PLE 0.16; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.04; PME-PME 0.06; PME-PLE 0.06. MOQ. AME-PME 0.38; AME-AME 0.28; PME-PME 0.38. Clypeus & chilum.

Clypeus 0.6 high; chilum divided. *Legs*. Length formula 4123; femora I, II with 1 row, III, IV with 2 rows of long, thin setae ventrally. *Male palp* (Figs. 94, 95, 107). RCF deep, reaches over tip of cymbium; from lateral view cymbium extremely bent, with weak dorsal scopula and a few strong spines apically. LTA with a long vertical stalk and irregular horizontal plate; DTA a flattened stalk; VTA long, with sharp tip. Tibiae short with 2 long prolateral setae; DTiA as long as ventrolateral one, hooked; VTiA (Fig. 95).

Female (paratype QM S51517). Total length 6.16; carapace 3 long, 2.04 wide; 1.12 high; cl/cw 1.47; sternum 1.48 long, 1.28 wide; sl/sw 1.16. Abdomen 3.16 long, 2.16 wide. Colour. Same as male. Eyes. Eye group width 0.5 of headwidth; AME 0.12; ALE 0.16; PME 0.16; PLE 0.16; AME–AME 0.06; AME–ALE 0.04; ALE–PLE 0.04; PME–PME 0.06; PME–PLE 0.06. MOQ: AME–PME 0.40; AME–AME 0.30; PME–PME 0.38. Clypeus 0.6 high. Legs. Same as male. Epigyne (Figs. 139, 140). With small, paired, halfmoon-shaped openings and a medial, lanceolate hook. Vulva with long, spiralled copulatory ducts ending in small almost touching spermathecae.

**Distribution**. New South Wales (Fig. 141).

**Etymology**. Species name is chosen because of the extremely long DTA which functions as a conductor.



Figs. 92–97. *Habronestes pictus* species-group male palps, ventral view (above), lateral view (below): (92, 93) *Habronestes pictus* (Koch); (94, 95) *Habronestes longiconductor* n.sp.; (96, 97) *Habronestes giganteus* n.sp. Scales 0.5 mm.

# Habronestes minor n.sp.

Figs. 62, 84, 85, 103, 127, 128, 141

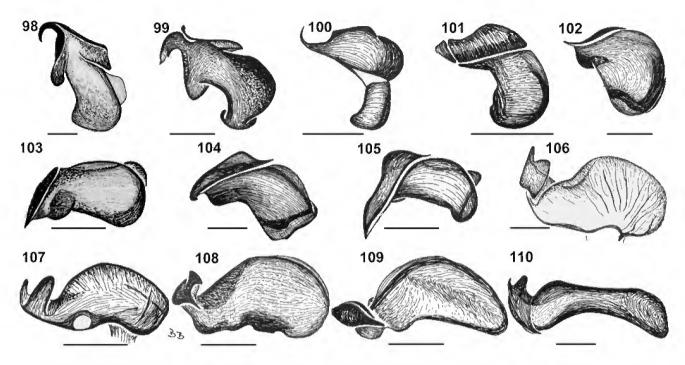
**Type material.** Holotype ♂: NSW, Booti Booti NP, 32°16′15″S 152°31′42″E, 9.x.1997, L. Wilkie, AM KS55916. Paratypes: NSW: 1♂ Booti Booti NP, 32°16′15″S 152°31′42″E, 13.xii.1996, L. Wilkie, AM KS56175; 2♂♂ as previous, AM KS56098 and AM KS56099; 1♀ as previous, 13.xii.1996, AM KS56100; 3♂♂ as previous in AM: KS56101, KS56102, KS56103; 1♂ as previous, 9.x.1997, AM KS56097; 1♂ Booti Booti NP, 32°16′47″S 152°31′28″E, 13.xi.1996, L. Wilkie, AM KS56092; 4 in AM as previous: 1♀ KS56093, 1♂ KS56095, 2♀ coll. 13.xii.1996, KS56094 and KS56096; 2♂♂ in AM, 700 m E of Wallaces Gap, Bendoura SF, 35°34′37″S 149°41′16″E, 16.iii.1999, J. Tarnawski & S. Lassau, KS55875 and KS55873; 1♂ North Head Rd, Murramarang NP, 35°42′25″S 150°16′30″E, 17.iii.1999, L. Wilkie, R. Harris & H. Smith, AM KS55874.

**Diagnosis**. Eyes in 2 rows, both rows procurved, AME smallest, other eyes subequal. One of the 3 smallest species, with 2 pairs of white patches on anterior part of abdomen and 1 or 2 patches in front of spinnerets, differs from *H. piccolo* and *H. wilkiei* by shape of tibial apophysis, cymbium extremely bent, RCF nearly reaches tip.

**Description**. *Male* (holotype). Total length 3.28; carapace 1.68 long, 1.28 wide; 0.64 high; cl/cw 1.31; sternum 0.80 long, 0.76 wide; sl/sw 1.05. Abdomen 2.08 long, 1.52 wide. *Colour*. Carapace, sternum sepia brown, iridescent; chelicerae medium brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 2 pairs of white patches on anterior part and 1 or 2 patches in front of spinnerets; laterally with 2 stripes equal in length; ventrally

pink brown. Legs pale brown; clearly annulated; legs I–IV white coxa, medium brown trochanter, proximal margin of femora sepia brown, proximal 1/2 white and distal 1/2 sepia brown, darker brown lateral stripes on patella and tibia. Eyes. In 2 rows each with 4 eyes, both rows procurved. AME smallest, other eyes equal. Eye group width 0.57 of headwidth; AME 0.07; ALE 0.08; PME 0.08; PLE 0.08; AME-AME 0.02; AME-ALE 0.02; ALE-PLE 0.02; PME-PME 0.04; PME-PLE 0.06. MOQ: AME-PME 0.24; AME-AME 0.16; PME-PME 0.20. Clypeus & chilum. Clypeus 0.28 high; chilum undivided, short. Legs. Length formula 4123; femora I, II with 1 row, III, IV with 2 rows of long thin setae ventrally. Male palp (Figs. 84, 85, 103). RCF deep, reaching tip of cymbium. LTA with a thick short vertical stalk and irregular horizontal plate, birdhead shape retrolaterally; DTA, with long, thin stalk; VTA long, with sharp tip. Tibiae short, a small hook between; DTiA with sharp tip, as long as tibia; VTiA (Fig. 85).

Female (paratype AM KS56094). Total length 3.76; carapace 1.68 long, 1.04 wide; 0.76 high; cl/cw 1.61; sternum 0.72 long, 0.68 wide; sl/sw 1.05. Abdomen 1.60 long, 1.08 wide. Colour. Same as male. Eyes. Eye group width 0.57 of headwidth; AME 0.08; ALE 0.10; PME 0.10; PLE 0.10; AME-AME 0.02; AME-ALE 0.02; ALE-PLE 0.02; PME-PME 0.04; PME-PLE 0.06. MOQ: AME-PME 0.22; AME-AME 0.18; PME-PME 0.24. Clypeus 0.36 high. Epigyne (Figs. 125, 126). With triangular scape. Vulva with long, spiralled copulatory ducts ending in large spermathecae.



Figs. 98–110. Habronestes pictus species-group male palps, LTA ventral view: (98) Habronestes bradleyi (Pickard-Cambridge); (99) Habronestes grayi n.sp.; (100) Habronestes piccolo n.sp.; (101) Habronestes jocquei n.sp.; (102) Habronestes grahami n.sp.; (103) Habronestes minor n.sp.; (104) Habronestes helenae n.sp.; (105) Habronestes wilkiei n.sp.; (106) Habronestes giganteus n.sp.; (107) Habronestes longiconductor n.sp.; (108) Habronestes pictus (Koch); (109) Habronestes raveni n.sp.; (110) Habronestes hunti n.sp. Scales 0.25 mm.

**Distribution**. Coastal New South Wales (Fig. 141).

**Etymology**. Species name refers to the small size of the species (Latin, *minor* = small).

#### Habronestes monocornis n.sp.

Figs. 54, 76, 77, 117, 118, 142

**Type material.** HOLOTYPE &: NSW, Gubatta, 33°38'7"S 146°33'12"E, 24.ii.1999, DD, QM S50906. PARATYPES:  $5\mbox{\ensuremath{$\circ$}}$  Same data as holotype in QM: S50906, S51518;  $2\mbox{\ensuremath{$\circ$}}$  Gubatta, 33°38'10"S 146°33'8"E, 24–28.ii.1999, DD, QM S51555, S52135;  $10\mbox{\ensuremath{$\circ$}}$ , 23 & & Pulletop, 33°58'46"S 146°3'28"E, 24–28.ii.1999, DD, QM S39855, S41546, S50992, S51504, S51590, S51603, S51604;  $1\mbox{\ensuremath{$\circ$}}$ , 1 & as previous, AM KS83926;  $1\mbox{\ensuremath{$\circ$}}$ , 21 & & Taleeban Woodland, 33°55'33"S 146°28'23"E, 23–27.ii.1999, DD, QM S39853, S51008, S51625.

**Diagnosis**. Eyes in circular group around AME; AME smallest, other eyes subequal. Abdomen with 2 pairs of white patches on anterior part and 3 patches in front of spinnerets. DTiA large, but basally not longer than tibia. LTA with 1 horn retrolaterally. Epigyne with large, paired, half moon shaped plates, not touching medially.

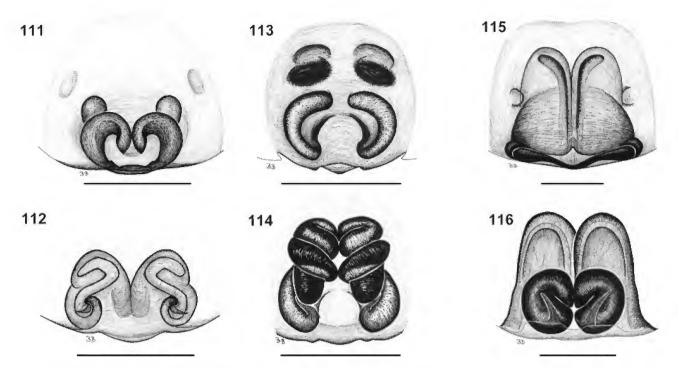
**Description**. *Male* (holotype). Total length 4.60; carapace 2.36 long, 1.84 wide; 1.00 high; cl/cw 1.28; sternum 1.20 long, 0.96 wide; sl/sw 1.25. Abdomen 2.24 long, 1.56 wide. *Colour*. Carapace, sternum sepia brown, iridescent; chelicerae medium brown; maxillae and labium medium brown, distally white. Abdomen sepia brown with 2 pairs of white patches and 3 patches in front of spinnerets; laterally with 3 long and broad white patches. Legs medium brown; clearly annulated; legs I–IV with white coxa, distally sepia brown, sepia brown trochanter, proximal about ½

white and distal ½ sepia brown femur, darker brown lateral stripes on patella and tibia; femur I proximal margin sepia brown with u-shaped pattern. Eyes. In circular group around AME. AME smallest, other eyes subequal. Eye group width 0.65 of headwidth; AME 0.08; ALE 0.18; PME 0.18; PLE 0.18; AME-AME 0.04; AME-ALE 0.10; ALE-PLE 0.08; PME-PME 0.08; PME-PLE 0.08. MOQ: AME-PME 0.42; AME-AME 0.20; PME-PME 0.44. Clypeus & chilum. Clypeus 0.44 high; chilum undivided, long. Legs. Length formula 4123; femora I, II with 1 row, III, IV with 2 rows of long thin setae ventrally. Male palp (Figs. 76, 77). RCF deep, 3/3 of the cymbium length. LTA with a thick, short vertical stalk and an irregular, horizontal plate with 1 horn retrolaterally; DTA with a thin stalk; VTA, broad with sharp tip. Tibiae short; DTiA large, but basally not longer than tibia; VTiA (Fig. 77).

Female (paratype QM S51590). Total length 5.12; carapace 2.28 long, 1.64 wide; 0.76 high; cl/cw 1.39; sternum 1.16 long, 1.00 wide; sl/sw 1.16. Abdomen 2.84 long, 1.96 wide. Colour. Same as male. Eyes. Eye group width 0.70 of headwidth; AME 0.08; ALE 0.18; PME 0.18; PLE 0.18; AME-AME 0.06; AME-ALE 0.10; ALE-PLE 0.10; PME-PME 0.08; PME-PLE 0.10. MOQ: AME-PME 0.44; AME-AME 0.22; PME-PME 0.44. Clypeus 0.44 high. Epigyne (Figs. 117, 118). With paired, half moon shaped plates. Vulva with long, spiralled copulatory ducts ending in almost touching spermathecae.

**Distribution**. Western New South Wales (Fig. 142).

**Etymology**. The choice of species name is a reference to the single horn on the retrolateral part of the LTA in the male palp.



Figs. 111–116. *Habronestes pictus* species-group epigynes, ventral view (above), vulvae, dorsal view (below): (111, 112) *Habronestes jocquei* n.sp.; (113, 114) *Habronestes bradleyi* (Pickard-Cambridge); (115, 116) *Habronestes hunti* n.sp. Scales 0.5 mm.

# Habronestes piccolo n.sp.

Figs. 66, 80, 81, 100, 121, 122, 143

**Type material.** HOLOTYPE ♂: NSW, Barrington SF, Tugalow Ck, Barrington Trail, E side of trail, 31°54'41"S 151°26'39"E, 4.ii–9.iv.1993, 1370 m, G/C, AM KS39146. PARATYPES: 1♀, 2♂♂, same data as holotype, AM KS39146; 1♂ Barrington Tops SF, W of jnctn of Thunderbolts Track & Devil's Hole track, 31°54'56"S 151°28'37"E, 4.ii–9.iv.1993, 1420 m, G/C, AM KS39144.

**Diagnosis.** Eyes in 2 rows, both rows procurved, PME and PLE largest. Most tiny of 3 smallest species with 2 pairs of white patches on anterior part of abdomen and 1 or 2 patches in front of spinnerets, differs from *H. wilkiei* and *H. minor* by shape of dorsal and retrolateral tegular apophysis and epigyne with lanceolate median scape.

**Description**. *Male* (holotype). Total length 2.62; carapace 1.36 long, 1.00 wide; 0.56 high; cl/cw 1.36; sternum 0.74 long, 0.68 wide; sl/sw 1.09. Abdomen 1.26 long, 0.96 wide. Colour. Carapace, sternum sepia brown; chelicerae medium brown; maxillae pale brown, at margin mottled with darker brown; labium pale brown, base darker brown. Abdomen sepia brown with 2 pairs of white patches and 3 patches in front of spinnerets; laterally with 2 equally long white stripes. Legs yellow brown; clearly annulated; legs I-IV with white coxa, prolateral suture sepia brown, sepia brown trochanter, proximal 1/3 of femora white and distal 2/3 sepia brown, darker brown lateral stripes on patella and tibia; femur IV proximal ½ white distal ½ sepia brown. Eyes. In 2 rows each with 4 eyes, both rows procurved. PME, PLE largest. Eve group width 0.50 of headwidth; AME 0.06; ALE 0.06; PME 0.09; PLE 0.09; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.02; PME-PME 0.04; PME-PLE 0.06. MOQ: AME-PME 0.24; AME-AME 0.16; PME-PME 0.22. Clypeus & Chilum. Clypeus 0.28 high; chilum undivided, long. Legs. Length formula 4132; metatarsi I, II with 1 row; III, IV with 2 rows of short modified ventral spines. *Male palp* (Figs. 80, 81, 100). RCF deep, ½ of the cymbium length. LTA with a long, broad, horizontal stalk, and semicircular plate with long, sharp tip retrolaterally; DTA with short, thin stalk; VTA long with rounded tip. Tibiae short; DTiA with a sharp, dorsally elongate, tip; VTiA (Fig. 81).

Female (paratype AM KS39146). Total length 3.32; carapace 1.48 long, 1.00 wide; 0.68 high; cl/cw 1.48; sternum 0.62 long, 0.74 wide; sl/sw 0.84. Abdomen 1.84 long, 1.28 wide. *Colour*. Same as male. *Eyes*. Eye group width 0.50 of headwidth; AME 0.06; ALE 0.06; PME 0.09; PLE 0.09; AME–AME 0.04; AME–ALE 0.04; ALE–PLE 0.02; PME–PME 0.04; PME–PLE 0.06. MOQ: AME–PME 0.24; AME–AME 0.16; PME–PME 0.22. Clypeus 0.38 high. *Epigyne* (Figs. 121, 122). With lanceolate median scape. Vulva with oval copulatory ducts ending in small globular spermathecae.

**Distribution**. Northeastern New South Wales (Fig. 143)

**Etymology**. Species name refers to the extremely small size of the species (Latin, *piccolo* = tiny).

## Habronestes pictus (L. Koch, 1865)

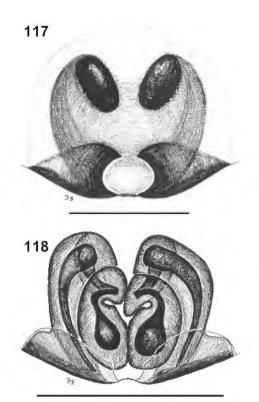
Figs. 67, 92, 93, 108, 133-135, 143

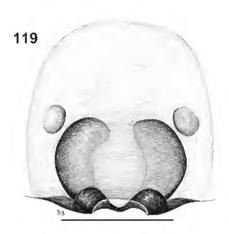
Enyo picta L. Koch, 1865: 861 (description female).

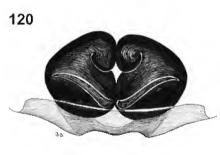
Habronestes pictus.-L. Koch, 1872: 311 T XXV figs. 3, 3a-c (description female); Jocqué, 1995: 143.

Storena picta.-Simon, 1893: 427.

**Remarks.** Habronestes pictus is the earliest known Habronestes species, described as Enyo picta by L. Koch (1865). The holotype of Enyo picta L. Koch is mentioned in Jocqué (1995) as lost. Dr Gisela Rack with R. Raven rediscovered the specimen in 1998 in the collection of







Figs. 117–120. *Habronestes pictus* species-group epigynes, ventral view (above), vulvae, dorsal view (below): (117, 118) *H. monocornis* n.sp.; (119, 120) *Habronestes raveni* n.sp. Scales 0.5 mm.

Zoologisches Museum Hamburg as a part of the Godeffroy Collection. It is the same female from Wollongong, NSW, described as *Enyo picta* by L. Koch in 1865 and as *Habronestes pictus* by L. Koch in 1872 (Fig. 133).

**Type material**. Holotype ♀ NSW: Wollongong, Godeffroy expedition (ZMH).

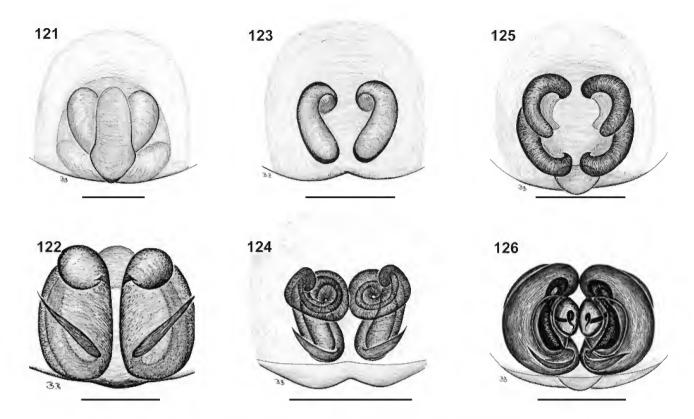
Material examined. NSW: 6♂♂ Tinderry Nature Reserve, northern entrance, 35°37'44"S 149°12'57"E, 14.iii.1999, L. Wilkie, R. Harris & H. Smith, AM KS55869; 2♂♂ Booti Booti NP, 32°16'15"S 152°31'42"E, 25.xi.1997, L. Wilkie, AM KS55956; 3♂♂ 13.xii.1996, AM KS55957; 1♂ Booti Booti NP, 32°14'44"S 152°32'33"E, 14.xii.1996, L. Wilkie, AM KS55963; 1♂ as previous, AM KS56091; 1♂ as previous, 25.xi.1997, AM KS55942; 1♂ Mt Bollard, Tallaganda SF, 35°39'14"S 149°28'44"E, 15.iii.1999, J. Tarnawski & S. Lassau, AM KS55864; 1♀, 2♂♂ Warra SF, 2.8 km W of Moggs Swamp Ck, Moggs Swamp Fire Tr. 20°59'19"S 151°57'14"E, 4.ii–9.iv.1993, 1140 m, G/C, AM KS36359; 3♂♂ Warra SF, Moggs Swamp Ck, Moggs Swamp Fire Trail, 29°58'47"S 151°58'29"E, 4.ii–9.iv.1993, 1080 m, G/C, AM KS36353; 4♂♂ Warra SF, Moggs Swamp Fire Trail, 2.5 km N of Moggs Swamp Ck, 29°57'32"S 151°58'18"E, 4.ii–9.iv.1993, 1170 m, G/C, AM KS36369. ACT: 4♂♂ Tidbinbilla, 35°26'S 148°56'E, 1978, AM KS6242.

**Diagnosis.** Eyes in 2 rows, both rows procurved, PME and PLE largest. Abdomen with 5 pairs of white patches on top, 3 pairs of elongate patches, 2 pairs of circular and 1 undulating patch in front of spinnerets.

**Description**. *Male*, AM KS55869. Total length 6.24: carapace 3.04 long, 2.00 wide; 3.2 high; cl/cw 1.52; sternum 1.48 long, 1.28 wide; sl/sw 1.15. Abdomen 3.04 long, 2.00 wide. Colour. Carapace, sternum and chelicerae sepia brown, iridescent; maxillae, labium sepia brown, distally white. Abdomen sepia brown, iridescent; with 5 pairs of white patches on top, 3 pairs long, 2 pairs circular and 1 undulating patch in front of spinnerets; laterally with 1 undulating, horizontal white stripe; ventrally, 1 longitudinal white stripe from epigastric fold to near tracheal spiracle. Legs yellow; clearly annulated; legs I-IV with white coxa, prolateral suture sepia brown, sepia brown trochanter, sepia brown femora and proximal white patch with darker brown lateral stripes on patella and tibia; femur II with proximal 1/3 white and distal 3/3 sepia brown; femora III, IV with proximal 1/2 of femora white and distal 1/2 sepia brown; with darker brown lateral stripes on patella and tibia. Eyes. In 2 rows each with 4 eyes, both rows procurved. PME and PLE largest, subequal. Eye group width 0.50 of headwidth; AME 0.12; ALE 0.12; PME 0.18; PLE 0.20; AME-AME 0.04; AME-ALE 0.04; ALE-PLE 0.04; PME-PME 0.12; PME-PLE 0.12. MOQ: AME-PME 0.56; AME-AME 0.28; PME–PME 0.48. *Clypeus & chilum*. Clypeus 0.84 high; chilum divided. Legs. Length formula 4123. Male palp (Figs. 92, 93, 108). RCF deep, almost running the entire cymbium length. LTA with long vertical stalk and irregular horizontal plate; DTA with flattened stalk; VTA long, with sharp tip. Tibia short; DTiA 1.5 as long as tibia, hooked; VTiA (Fig. 93).

Female (paratype AM KS36359). Total length 7.52; carapace 3.36 long, 2.36 wide; 1.68 high; cl/cw 1.42; sternum 1.48 long, 1.48 wide; sl/sw 1.00. Abdomen 4.16 long, 3.00 wide. Colour. As in male. Eyes. Eye group width 0.50 of headwidth; AME 0.12; ALE 0.12; PME 0.20; PLE 0.20; AME-AME 0.06; AME-ALE 0.06; ALE-PLE 0.09; PME-PME 0.14; PME-PLE 0.12. MOQ: AME-PME 0.6; AME-AME 0.30; PME-PME 0.54. Clypeus 0.84 high. Epigyne (Figs. 133–135). With undulate posterior margin and undulate plate. Copulatory ducts anteriorly visible through the tegument. Vulva with long, spiralled copulatory ducts ending in pear-shaped, touching spermathecae.

**Distribution**. Northeastern New South Wales and ACT (Fig. 143).



Figs. 121–126. *Habronestes pictus* species-group epigynes, ventral view (above), vulvae, dorsal view (below): (121, 122) *Habronestes piccolo* n.sp.; (123, 124) *Habronestes wilkiei* n.sp.; (125, 126) *Habronestes minor* n.sp. Scales 0.25 mm.

#### Habronestes raveni n.sp.

Figs. 57, 78, 79, 109, 119, 120, 143

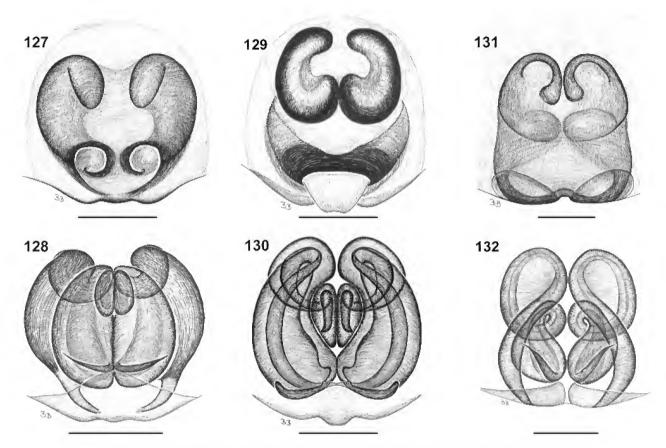
Type material. HOLOTYPE &: NSW, Tinderry Nature Reserve, southern entrance, 35°39'39"S 149°12'43"E, 14.iii.1999, J. Tarnawski & S. Lassau, AM KS55892. PARATYPES: NSW: 2 & & 0.5 km from Wheatley Ck Rd on Camp Ck Rd, leasehold land, 28°47'0"S 152°19'29"E, 4.ii-9.iv.1993, 550 m, G/C, AM KS36269; 1& as previous, AM KS56173; 1 d East Kunderang Trail, 1.35 km E of West Kunderang Trail, 30°48'41"S 152°2'55"E, 4.ii–9.iv.1993, 890 m, G/C, AM KS39163; 31 ♂ ♂ Kunderang Trail, 1.2 km from homestead, 30°49'12"S 152°8'3"E, 4.ii–9.iv,1993, 210 m, G/C, AM KS39167; 19, 13 Kunderang Trail, 1.85 km from homestead, 50 m S of Wonga Gully, 30°48'56"S 152°7'44"E, 4.ii-9.iv.1993, 210 m, G/C, AM KS39029; 3♂♂ as previous, AM KS39165; 7 さ Kunderang Trail, 3.45 km from homestead, 30°48'29"S 152°7'7"E, 4.ii–9.iv.1993, 280 m, G/C, AM KS39138; 13 ♂ ♂ NE facing slope above Kunderang Stn Ck, 30°48'26"S 152°6'26"E, 4.ii-9.iv.1993, 410 m, G/C, AM KS39166; 1& Pulletop, 34°0'6"S 146°5'10"E, 24-28.ii.1999, DD, OM S50994; 1♀, QM S50995; 4♂♂ Ramornie SF, track off Mt Tindal Rd, 29°42'38"S 152°38'9"E, 4.ii–9.iv.1993, 200 m, G/C, AM KS39137; 288, AM KS55965; 788 Richmond Range SF, Wattle Ck Rd, 28°38'42"S 152°46'29"E, 4.ii-9.iv.1993, 220 m, G/C, AM KS36062; 1 & Scotts Main Range, 33°56'S 150°18'E, with nest, AM KS50421; 93 3 Second gully N of Wonga Gully, 30°48'39"S 152°7'26"E, 4.ii-9.iv.1993, 270 m, G/C, AM KS39164; 1♀, 6♂♂ Taleeban Woodland, 33°56'29"S 146°25'8"E, 23–27.ii.1999, DD, QM S50913; 2♀♀, 3♂♂, QM S51006; 1 ♂, QM S52129; 1 ♀, 5 ♂ ♂, QM S52133; 2 ♂ ♂ Ungarie SF, 33°39'44"S 147°4'6"E, 25.iii.1996, Callitris forest F2 trap B2, 21-28 Mar 1996, D. Smith & R. Harris, AM KS49594; 1 

Boundary Creek SF, 29°56'48"S 152°33'27"E, 9.iv.1993, 4.ii-9.iv.1993, 600 m, G/C, AM KS56170.

**Diagnosis.** Eyes in circular group around AME; AME smallest, other eyes equal. Abdomen with 3 pairs of white patches on anterior part and 2 or 3 patches in front of spinnerets.

**Description**. *Male* (holotype). Total length 5.72; carapace 2.84 long, 2.20 wide; 1.24 high; cl/cw 1.29; sternum 1.52 long, 1.24 wide. Abdomen 2.88 long, 2.04 wide. Colour. Carapace and chelicerae sepia brown; sternum orange brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 3 irregular pairs of white patches on anterior part and 3 patches in front of spinnerets; laterally with 2 long white stripes equal in length; ventrally pink brown. Legs medium brown; clearly annulated; legs I, II with white coxa, distal angles sepia brown, sepia brown trochanter, sepia brown femur, darker brown lateral stripes on patella and tibia; femora III, IV with proximal 1/3 of white and distal 3/3 sepia brown. Eyes. In circular group around AME. AME smallest, other eyes equal. Eye group width 0.55 of headwidth; AME 0.12; ALE 0.18; PME 0.18; PLE 0.18; AME-AME 0.04; AME-ALE 0.08; ALE-PLE 0.06; PME-PME 0.08; PME-PLE 0.12. MOQ: AME-PME 0.48; AME-AME 0.28; PME–PME 0.44. Clypeus & chilum. Clypeus 0.6 high; chilum undivided, long. Legs. Length formula 4123. Male palp (Figs. 78, 79, 109). RCF deep, almost running the entire cymbium length. LTA with a long vertical stalk and with an irregular horizontal plate, bird head shape retrolaterally; DTA with a thin stalk; VTA long, with sharp tip. Tibia short; DTiA as long as ventrolateral one; VTiA (Fig. 79).

Female (paratype QM S52129). Total length 7.00; carapace 3.40 long, 2.44 wide; 1.48 high; cl/cw 1.39; sternum 1.60 long, 1.40 wide; sl/sw 1.14. Abdomen 3.60 long, 3.00 wide. Colour. Same as male. Eyes. Eye group width 0.55 of headwidth; AME 0.14; ALE 0.20; PME 0.20; PLE 0.20;



Figs. 127–132. *Habronestes pictus* species-group epigynes, ventral view (above), vulvae, dorsal view (below): (127, 128) *Habronestes helenae* n.sp.; (129, 130) *Habronestes grahami* n.sp.; (131, 132) *Habronestes grayi* n.sp. Scales 0.25 mm.

AME-AME 0.04; AME-ALE 0.08; ALE-PLE 0.08; PME-PME 0.12; PME-PLE 0.12. MOQ: AME-PME 0.54; AME-AME 0.32; PME-PME 0.52. Clypeus 0.72 high. *Epigyne* (Figs. 119, 120). Posterior margin undulate, with central opening at posterior margin. Vulva with kidney-shaped, medially touching copulatory ducts ending in globular spermathecae anteriorly.

**Distribution**. Northeastern to western New South Wales (Fig. 143).

**Etymology**. Named in honour of Dr Robert J. Raven of the Queensland Museum, in esteem for his important work on Australian spiders.

#### Habronestes wilkiei n.sp.

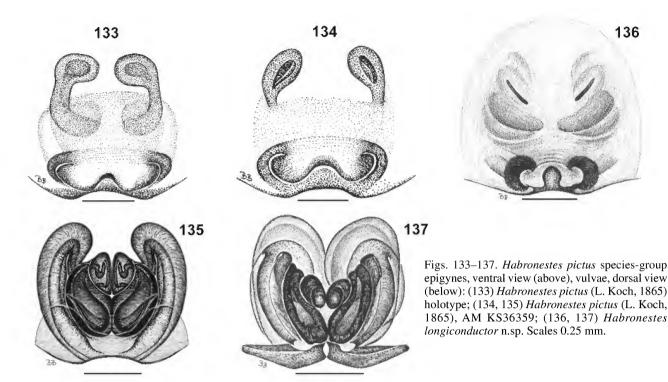
Figs. 63, 82, 83, 105, 123, 124, 143

**Type material.** Holotype ♂: NSW, Wyrrabalong NP, 33°16'47"S 151°32'40"E, 15.xii.1996, L. Wilkie, AM KS55931. Paratypes: 1♀ Munmorah SRA, 33°12'34"S 151°34'59"E, 17.xi.1996, L. Wilkie, AM KS55951; 3 in AM as previous: 1♀ KS55973, 1♂ KS56137, 1♀ KS56138, 4 in AM as previous but coll. 16.xii.1996: 1♂ KS56139, 1♂ KS56134, 1♂ KS56141, 1♂ KS56142; 1♂ Munmorah SRA, 33°12'26"S 151°34'37"E, 17.xi.1996, L. Wilkie, AM KS55977; 1♀ as previous, AM KS56130; 8 as previous: 1♀ AM KS55925, 1♀ 4♂ AM KS56004, 1♀ 1♂ QM S60829; 1♀ Munmorah SRA, 33°13'9"S 151°34'15"E, 17.xi.1996, L. Wilkie, AM KS55975; 1♂ as previous, AM KS56125; 3 in AM as previous troll. 1♂ KS56126, 1♂, KS56127; 1♀, KS56128; 1♀, 1♂ Wyrrabalong NP, 33°16'44"S 151°32'51"E, 15.xii.1996, L. Wilkie, AM KS56153; 2♂ ♂ in AM as previous: KS56155 and KS56156; 3 as previous but coll. 16.xi.1996: 1♂ KS56157, 1♀

KS56158, 1  $\circlearrowleft$  KS56154; 1  $\circlearrowleft$ , 1  $\circlearrowleft$  Wyrrabalong NP,  $33^{\circ}16'48"S$  151°32'45"E, 15.xii.1996, L. Wilkie, AM KS56164; 1  $\circlearrowleft$  2.v.1997, AM KS55936; 1  $\circlearrowleft$  27.xii.1997, AM KS55943; 4 in AM as previous: 1  $\circlearrowleft$  KS56032, 1  $\circlearrowleft$  KS56037, 1  $\circlearrowleft$  KS56050, 1  $\circlearrowleft$  KS56055; 1  $\circlearrowleft$  Wyrrabalong NP,  $33^{\circ}16'51"S$  151°32'37"E, 16.xi.1996, L. Wilkie, AM KS56165; 1  $\circlearrowleft$  2.v.1997, AM KS55980; 1  $\circlearrowleft$  , AM KS56054.

**Diagnosis**. Eyes in 2 rows, both rows procurved, AME smallest, other eyes equal. One of the 3 smallest species, with 2 pairs of white patches on anterior part of abdomen and 1 or 2 patches in front of spinnerets, differs from *H. piccolo* and *H. minor* by shape of DTA and LTA.

**Description**. *Male* (holotype). Total length 3.04; carapace 1.60 long, 1.12 wide; 0.56 high; cl/cw 1.42; sternum 0.80 long, 0.76 wide; sl/sw 1.05. Abdomen 1.44 long, 1.00 wide. Colour. Carapace sepia brown; sternum yellow brown; chelicerae medium brown; maxillae and labium pale brown, distally white. Abdomen sepia brown with 2 pairs of white patches on anterior part and 1 patch in front of spinnerets; laterally 2 long white stripes, first one broad; ventrally pink brown. Legs yellow brown; clearly annulated; legs I-IV with white coxa, sepia brown trochanter, proximal margin of femora sepia brown, proximal ½ white and distal ½ sepia brown, darker brown lateral stripes on patella and tibia. Eyes. In 2 rows each with 4 eyes, both rows procurved. AME smallest, other eyes equal. Eye group width 0.58 of headwidth; AME 0.06; ALE 0.09; PME 0.09; PLE 0.09; AME-AME 0.02; AME-ALE 0.03; ALE-PLE 0.03; PME-PME 0.04; PME-PLE 0.04. MOQ: AME-PME 0.24; AME-



AME 0.14; PME–PME 0.22. Clypeus & chilum. Clypeus 0.28 high; chilum undivided, short. Legs. Length formula 4123. Male palp (Figs. 82, 83, 105). Cymbium RCF deep, almost running the entire cymbium length. LTA with a thick, short, vertical stalk and with irregular horizontal plate, birdhead shape retrolaterally; DTA with a thin stalk; VTA long, with rounded tip. Tibiae short; DTiA with chitinous rim, as long as VTiA (Fig. 83).

Female (paratype AM KS55925). Total length 3.76; carapace 1.72 long, 1.16 wide; 0.72 high; cl/cw 1.48; sternum 0.80 long, 0.76 wide; sl/sw 1.05. Abdomen 2.04 long, 1.52 wide. Colour. Same as male. Eyes. Eye group width 0.60 of headwidth; AME 0.06; ALE 0.09; PME 0.09; PLE 0.09; AME-AME 0.04; AME-ALE 0.03; ALE-PLE 0.04; PME-PME 0.06; PME-PLE 0.06. MOQ: AME-PME 0.26; AME-AME 0.16; PME-PME 0.24. Clypeus 0.28 high. Epigyne (Figs. 123, 124). With sausage-like spermathecae in heart-shaped pattern visible through the tegument. Vulva with anteriorly curled copulatory ducts ending in long separated sausage-like spermathecae.

**Distribution**. Northeastern New South Wales (Fig. 143).

**Etymology**. Species name is a patronym in honour of Mr Lance Wilkie, who collected the holotype.

# Discussion

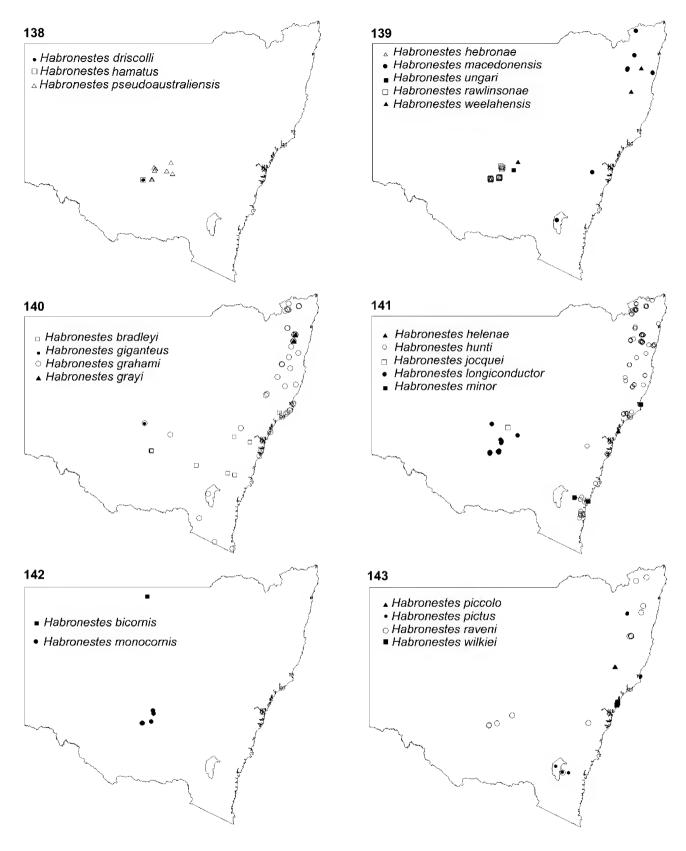
The definition of Australian zodariid genera has been based mainly on genitalic characters (Baehr & Jocqué, 2001). Epigynes are less informative, mainly because there are no unique apomorphies recognized yet. In Habronestes, as well as in other genera of zodariids, male palps therefore remain the main characters to define the genera as well as the species. This is the first part of an ongoing revision of the genus Habronestes, which now contains 28 species. All uniquely share the retrolateral cymbial fold (RCF), the sickle-shaped VTA and the DTA with long stalk and curled apical end covered with spicules (Figs. 1-6) in male palp. In addition, all possess 2 lines of short, ventral spines on tarsi I-IV, a distoventral preening brush on metatarsi II, III and long, strong spines on tibiae and metatarsi III and IV. The lines of tarsal spines have not been reported elsewhere in the Zodariidae and I suggest they constitute a further synapomophy of *Habronestes*. However, the abdominal pattern—2–5 pairs of white patches on top, and 1–3 patches in front of spinnerets on dark brown abdomen—occur also in other genera such as Asteron and Storena.

This is the first time that *Habronestes* has been broken up into species groups. The three species groups here recognized are founded on somatic characters—different eye sizes, cephalic profile, spination—that show some congruence with genitalic characters. Synapomorphies for the three species-groups are:

Habronestes australiensis species-group: Carapace raised in eye region. Eyes, PLE largest, 2–3× AME.

Habronestes macedonensis species-group: Carapace not raised in front; highest point just behind eye region. AME largest, eyes in 2 rows, both rows procurved. Femora III, IV with a row of 3–6 stout dorsal spines at distal end; patella III, IV with 1 irregular longitudinal row of stout spines prolaterally.

Habronestes pictus species-group: Carapace not raised in front; AME or PME never largest eyes. Eyes in 2 rows,



Figs. 138–143. New South Wales, showing collection localities: (138) species of *Habronestes australiensis* species-group; (139) species of *Habronestes macedonensis* species-group; (140–143) species of *Habronestes pictus* species-group.

both rows procurved or in circular group. All eyes nearly equal sized or AME smallest.

Nevertheless, similar male palps with extremely bent cymbium and enlarged retrolateral cymbial fold reaching the tip of cymbium occur in both the H. australiensis (H. driscolli) and H. pictus (H. longiconductor, H. giganteus) species-groups. To conclude that these similarities are synapomorphic would require considerable homoplasy in the somatic characters. In the Asteron complex (Baehr & Jocqué, 1996) similar extremely bent palps are found in several undescribed genera (B. Baehr, pers. obs.). Jocqué (1998) found that, in a number of spider genera, male palps increase in complexity in different species within the same genus. Examples of this have appeared many times in the course of the evolution of the palp. In any case, these palpal characters are an excellent demonstration of evolution within species-groups in Habronestes. I suggest that for at least the *H. australiensis* and *H. pictus* species-groups, the plesiomorphic condition is: palps with straight spoon-shaped cymbium and embolus with prolateral or basal origin. The derived condition is: palps with extremely bent cymbium and embolus with retrolateral origin on tegulum. It is unknown whether the derived condition is also present in the H. macedonensis species-group, as only the NSW species have been examined.

In contrast to the Asteron-complex, the genus Habronestes can be considered monophyletic, with its synapomorphies in the male palp: presence of RCF, well-developed LTA with stalk and plate, long sickle-shaped VTA and DTA with a thin long stalk and a curled end covered with spicules. long thin semicircular embolus. The phylogenetic relationships of the zodariid genera are still unknown. However, there are some obvious characters that suggest where the genus *Habronestes* fits. The putative sister group is Leptasteron, in which males can be recognized by the enormous DTA with stalk and a large terminal folded part, the very long bent VTA and the long whip-like embolus (Baehr & Jocqué, 2001, figs. 11D,E). These characters also occur in Habronestes but they are further derived with special synapomorphic shapes. According to this, Habronestes is a monophyletic genus in the paraphyletic Asteron-complex.

Further research is necessary to describe all species of the genus *Habronestes*. These investigations will provide detailed distribution patterns of each *Habronestes* species. Additional data will yield more information about the relationship between species and species groups and the origin of the genus *Habronestes* in Australia.

ACKNOWLEDGMENTS. I would like to thank the Australian Museum for a three month Fellowship and an Australian Biological Resources Study Grant, for supporting this project, Dr Michael Gray of the Australian Museum, for supporting the work, preparing the maps, locality data and providing critical comments on the manuscript, Mr Graham Milledge, the collection manager of Australian Museum Arachnology, who provided valuable technical assistance during this project, for help with the scanning electron microscope, Dr Robert Raven Queensland Museum (Brisbane), for being patient, my children Johanna and Ursula Baehr. I am also indebted to Mrs Wendy Hebron for the loan and sorting of additional material.

#### References

- Allan, R.A., M.A. Elgar & R.J. Capon, 1996. Exploitation of an ant chemical alarm signal by the zodariid spider *Habronestes* bradleyi Walckenaer. Proceedings of the Royal Society of London B 263: 69–73.
- Baehr, B., & R. Jocqué, 1996. A revision of *Asteron*, starring male palpal morphology (Araneae, Zodariidae). Proceedings of the XIII International Congress of Arachnology, Geneva, 3–8
  September 1995. *Revue suisse de Zoologie, hors serie* 1: 15–28.
- Baehr, B., & R. Jocqué, 2000. Revisions of the genera in the Asteron-complex (Araneae, Zodariidae). The new genera Cavasteron and Minasteron. Records of the Western Australian Museum 20: 1–30.
- Baehr, B., & R. Jocqué, 2001. Revisions of the genera in the *Asteron*-complex (Araneae, Zodariidae). The new genera *Pentasteron, Phenasteron, Leptasteron* and *Subasteron. Memoirs of the Queensland Museum* 46(2): 359–385.
- Dallwitz, M.J., T.A. Paine & E.J. Zurcher, 1998. Interactive keys. In *Information Technology, Plant Pathology and Biodiversity*, ed. P. Bridge, P. Jeffries, D.R. Morse and P.R. Scott, pp. 201–212. Wallingford: CAB International.
- Dunn, R.A., 1951. Spiders of the Russell Grimwade expedition. *Memoirs of the National Museum of Melbourne* 17: 9–18.
- Hogg, H.R., 1900. A contribution to our knowledge of the spiders of Victoria: including some new species and genera. *Proceedings of the Royal Society of Victoria* 13: 68–123.
- Jocqué, R., 1991. A generic revision of the spider family Zodariidae (Araneae). Bulletin of the American Museum of Natural History 201: 1–160.
- Jocqué, R., 1995. Notes on Australian Zodariidae (Araneae), II. Redescriptions and new records. Records of the Australian Museum 47(2): 141–160.
- http://www.amonline.net.au/pdf/publications/187.pdf [= Abstract]
- Jocqué, R., 1998. Female choice, secondary effect of «mate check»? A hypothesis. Belgian Journal of Zoology. 128: 99– 117.
- Jocqué, R., & B. Baehr, 1992. A revision of the Australian spider genus *Storena* (Araneae, Zodariidae). *Invertebrate Taxonomy* 6: 953–1004.
- Jocqué, R., & B. Baehr, 2001. Revisions of the genera in the Asteron-complex (Araneae, Zodariidae). Asteron Jocqué and the new genus Pseudasteron. Records of the Australian Museum 53(1): 21–36.
  - http://www.amonline.net.au/pdf/publications/1321\_complete.pdf
- Koch, L., 1865. Beschreibungen neuer Arachniden und Myriapoden. Verhandlungen der koeniglich kaiserlichen zoologischen-botanischen Gesellschaft in Wien: 857-892.
- Koch, L., 1872. Die Arachniden Australiens. *Nurnberg, I*, pp. 105–368.
- Kritscher, E., 1956. Bisher unbekannt gebliebene Araneen-Maennchen und Weibchen des Wiener Naturhistorischen Museums. (I. Teil). Annalen des naturhistorischen Museums zu Wien 61: 254–272.
- Petrunkevitch, A., 1928: Systema Aranearum. *Transactions of the Connecticut Academy of Arts and Sciences* 29: 1–270.
- Pickard-Cambridge, O., 1869. Descriptions and sketches of some species of Araneida, with characters of a new genus. *Annals and Magazine of Natural History* (4) III: 52–74.
- Rainbow, W.J., 1911. A census of Australian Araneidae. *Records of the Australian Museum* 9: 107–319.
- Simon, E., 1893. *Histoire naturelle des Araignées*. Paris 1(2) 1893: 257–488.

Manuscript received 25 September 2001, revised 1 December 2002 and accepted 24 March 2003.

Associate Editor: D.J. Bickel.

# NOTE FOR BINDERS

The Contents of Volume 55 (2003)\* will be published in Volume 56(1) due early in 2004

\* http://www.amonline.net.au/pdf/publications/1298.pdf

# INSTRUCTIONS TO AUTHORS

http://www.amonline.net.au/pdf/publications/authors.pdf

# CONTENTS

An appraisal of the cicadas of the genus Abricta Stal and allied genera (Hemiptera: Auchenorrhyncha: Cicadidae)	245
Dendroid and tuboid graptolites from the Llandovery (Silurian) of the Four Mile Creek area, New South Wales	
	305
The Triassic amphibian <i>Thoosuchus yakovlevi</i> and the relationships of the Trematosauroidea (Temnospondyli: Stereospondyli)	
Ross J. Damiani & Adam M. Yates	331
Revision of the Australian spider genus <i>Habronestes</i> (Araneae: Zodariidae).  Species of New South Wales and the Australian Capital Territory	
BARBARA BAEHR	343

